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ON REDUCTION DIVISION IN THE POLLEN-MOTHER-CELLS OF *CYANOTIS CRISTATA*

BY

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Udipi, South Kanara.

I. Introductory.

This paper sets forth the results of a study extending over a period of rather more than two years (1927–29) made by the writer on meiosis in the pollen-mother-cells of *Cyanotis cristata*, a member of the Natural Order *Commelinaceae*. This object was selected for detailed work after a preliminary study of a number of plants mainly on account of its special suitability for any form of the chrom-osmium technique, due to the minute size of the anthers, which, on the average are only a third of a millimetre long, a quarter broad, and a fifth in thickness: a very fine fixation is, therefore, possible with Flemming's mixture or its modifications, which, with all their merits, suffer from the single drawback of a low power of penetration and are occasionally failures for this reason. Furthermore, the genus *Cyanotis* is closely related to *Tradescantia*, which has been much used in cytological work and this was also a point which the writer had in mind when selecting this plant for detailed study.

II. Material and Methods.

Various species of *Cyanotis*, including *C. cristata* are among the commonest weeds on the west coast of Madras during the rainy months (June–October) and the supply of material is unlimited. Material was fixed on fourteen different occasions at various hours of the day from 7 a.m. to 5 p.m., after the usual preliminary examination of one anther from each flower-bud in acetic methyl-green or aceto-carmine. However, since in each flower-bud the different anthers are found to be at different stages in the course of meiotic division, such a preliminary examination is of a rather

limited value. At first, the weaker "Bonn" modification of Flemming's mixture (Strasburger's "Praktikum," 7 te Aufl., S. 65) was used for fixation, both at the room-temperature (24–27 degrees) and hot (50 degrees). The material being delicate, the action of this killing-agent was found to be too violent and disintegrating, the fault being chiefly due, no doubt, to the excessive amount of acetic acid contained in it. Further, structures that were artifacts beyond all question made themselves evident particularly in connection with the achromatic figure, especially when the hot fluid was used. Material fixed in the "Bonn" mixture was, therefore, discarded after a small number of anthers was sectioned and examined, and a modification containing 0.4 per cent chromic acid, 0.2 per cent osmic acid, and 1.0 per cent acetic acid in spring water of a very pure quality was used for fixation on the twelve subsequent occasions. As it was feared that the power of penetration of this mixture might be low on account of the reduced acetic acid content, the first few lots were fixed at a temperature of 35 degrees. It was soon found, however, that while fixation at this temperature certainly did no harm, such a course was not necessary, as the mixture worked very well at the room temperature. Fixation was carried out for 24 hours, washing done overnight, and dehydration effected by means of alcohol, starting with 5 per cent and rising by steps of 10 per cent at each change. Cedar-wood oil was used throughout as the intermedium, and the material finally imbedded in paraffin of a melting point of 56 degrees. Sections were made at a uniform thickness of 10 microns, although a few anthers, in the earlier stages of the work, were cut at 5 microns. Sections cut at 5 microns, however, were found to contain far too many cut nuclei to be really useful for study. For, barring exceptional cases, interpretation of such cut nuclei is more difficult and much more liable to error than it is in the case of nuclei which are entire and un-cut. The practice of making sections "as thin as possible" was, therefore, given up.

Iron-haematoxylin according to Heidenhain was the stain generally used, a strictly uniform technique being adopted throughout, so as to make sure that any variations observed in the staining reaction of the nuclear structures at the various stages represented real differences and were not due to merely accidental differences in the staining technique. No counter-stain for the plasma was used, nor was there need for any. Occasionally, gentian violet was also used for staining the nucleus, as a sort of control.

So far, 537 anthers have been cut into over 12,000 sections and studied. Among these, of course, especially as the work advanced, many contained repetitions of stages observed previously, but right

till the end of the work, stages not studied before continued to appear, giving a more complete seriation and a clearer insight into the processes concerned. As a matter of fact, it was only towards the conclusion of the work that the stages leading from the pachytene to the diffuse stage (Figs. 22–24) were first observed by the writer, and these are shown only by one single slide; while the seriation observed in this slide is adequate enough to leave no doubt as to the sequence of the stages, it does not give a sufficiently detailed picture of the transitional conditions between them. To this extent, therefore, there is a slight gap in the work, even after a careful study of over five hundred anthers.

III. Descriptive.

Origin of the leptonema.—The resting nucleus consists of a faintly staining reticulum and a large nucleolus which stains an intense black with haematoxylin. A few "net-knots" may be visible here and there where the strands of the reticulum cross. The first visible sign of the commencement of meiosis (Fig. 1) is the gradual accumulation of chromatin in certain strands of the reticulum, with its corresponding progressive withdrawal from the other portions, as a consequence of which, these latter ultimately disappear from view (Figs. 2, 3). The chromatin in these thickened and deeply-staining strands in its turn condenses into a number of 'chromocentres' (prochromosomes ?) which are spherical or spheroidal bodies staining an intense black with iron-haematoxylin (Fig. 3). The number of the chromocentres appears to be variable, but is certainly smaller than the diploid number of chromosomes characteristic of the species. The leptonema threads take their origin from the chromocentres as short strands with a very pronounced beaded structure; as the leptotene threads grow out of them, the chromocentres gradually diminish in size and ultimately disappear. The beaded structure represents probably the "chromomeres", believed to be the units of which the chromosomes are built up. While most of the chromocentres give rise to a single leptonema thread each, it is certain that more than one of the latter may be formed out of one chromocentre, as is shown for instance, in Fig. 3, top right-hand corner. Soon, the leptonema threads elongate very considerably, still retaining the beaded structure, but staining less and less deeply, and finally only a greyish brown; it looks as if the chromatin, becoming more and more diffused over continuously growing leptonema threads, suffers a corresponding diminution in the intensity of its staining reaction. In the meantime, the nuclear cavity has been enlarging and keeping pace with the growth of the leptonema threads; these are now a loose tangle of beaded strands,

forming to all outward appearance a continuous "spireme". It is not probable, however, that the spireme is really continuous at this stage. The clearly independent origin of the leptonema threads, without even the suggestion of a process whereby they could become connected together, as well as the fact that even in un-cut nuclei more than two free ends of the "spireme" can always be observed, all make it highly improbable that a continuous spireme is present at this stage. (Fig. 4).

Looping and Polarization of the leptonema threads.—When the changes noted above have been in progress, the nucleolus has been gradually shifting its position towards a side of the nuclear cavity and come to occupy a position very close to the nuclear membrane; often it is closely pressed against the latter and may then change its shape and appear lenticular in section. Many of the leptotene threads may now be observed to converge towards the nucleolus. This marks the commencement of a "polarization," which later becomes very pronounced, and persists till a late stage is in the prophase. The leptotene threads now begin to undergo a process of condensation, and the chromomeres gradually disappear from view. The threads shorten, one of the ends of each becomes definitely connected with the nucleolus and the threads become bent into loops (Fig. 5). It has not been possible to determine whether the other end of each thread also becomes connected with the nucleolus, after the thread is bent into a loop, but even if it does, it is only temporarily. Thus is established the "thin" or "leptonema bouquet", with the nucleolus at the base and the slender chromosomes bent into loops placed upon this base. It has not been possible to count the number of the loops accurately (Fig. 5).

As soon as this polarization of the leptonema threads with reference to the nucleolus takes place and connection between them is established, the leptotene threads rapidly gain in the intensity of their staining reaction, and the nucleolus suffers a corresponding loss, changing from the intense black of the earlier stages to a deep grey (with iron-hæmatoxylin). From this stage onwards, at any rate, it is perfectly certain that a "continuous spireme" is not present.

The synaptic union.—The leptotene threads now enter into synaptic union. Members of a pair come together side-by-side, (parasynapsis, Fig. 6) twist round each other and form a double spiral (Fig. 6). The twisting, which is rather loose at first, starts at the base and progresses upwards; as it becomes completed, it becomes tighter, first at the base, and then in the upper portions; finally it becomes uniformly close and tight throughout, and the component strands can no longer be distinguished.

Zygonema stage.—The nucleus has now entered upon the zygonema stage, and the changes following are very interesting. The nuclear cavity undergoes a very considerable expansion (Fig. 7) the cytoplasmic fluid evidently diffusing into it; such an ingress is probably permitted by a marked change in the permeability of the nuclear membrane at this stage. The chromosomes continue to gain steadily in the intensity of their staining reaction and change from a deep grey into an intense black. The nucleolus suffers a corresponding loss, and changes from a deep grey to at first a dirty brown, and finally a pale straw-colour, towards the end of the zygonema stage. More interesting still are the changes undergone by the chromosomes, evidently as a result of the progress in the tightening of the twist between the synaptic pairs. In the early zygonema, the synaptic double chromosomes are lax and flaccid bodies, forming graceful curves (Fig. 7), but in the more advanced conditions of this stage, they gradually become stiffer (Fig. 8) and assume a more and more erect position on the base formed by the nucleolus; towards the end of the zygonema they are found to have attained such a degree of stiffness that they assume an erect position and stand up on the base formed by the nucleolus (compare Figs. 7, 8, and 9). At the stage shown in Figure 9, the ends of the strands are still flaccid and hang down and interlock among one another, but at still later stages, as the spireme is preparing to enter into synizesis, this stiffening extends to the ends of the strands (Fig. 10). The significance of these changes and the possible part played by them in bringing about the "first contraction" the writer proposes to discuss in a later section of this paper.

Towards the late stages of the zygonema, the nuclear cavity undergoes a contraction (compare Figures 7 and 10); the cytoplasmic fluid must have retreated outside the nucleus once again.

Synizesis.—The nucleus now enters upon the synizesic condition. As the chromosomes are preparing to pass into the "first contraction", each twisted synaptic pair looks like a single thick strand, no indication whatever of its constitutional duality being perceptible in the entire and uninjured condition. Nevertheless, (as however happens but rarely) where the microtome knife has scraped along the surface of such a strand, specially near the free end, and thus broken the continuity of the two constituent threads at each turn or twist of the spiral, it is still possible to observe (Fig. 10) that the two threads have not become fused together, but have remained separate, and that they still continue to form a double spiral: evidently, it is the extreme closeness and regularity of the twist that is responsible for concealing the internal structure of the spireme-threads from our view in the uninjured strand.

The commencement of synizesis is marked by an expansion of the nuclear cavity (Fig. 11), this expansion continuing till a fairly advanced condition of this stage is reached. The chromosomes form at first a dense tangle, and ultimately a compact ball or knot made up of thick strands and enclosing the nucleolus, though portions of the latter may project out of the knot. Some of the strands of the spireme also may project out of the main mass in the form of hooks, loops, etc. Essentially the process which brings about the synizesic contraction seems to consist in a retraction of the free ends of the spireme threads towards the base (i.e., the nucleolar end) as a result of which the strands form at first a tangle and then a compact knot (Figs. 10 and 11).

The "first contraction" seems to last a good length of time, as suggested by the fact that the advanced stages of synizesis are shown by both loculi of an anther, while in the case of most other stages, the two compartments show different stages, one more or less in advance of the other: the duration of synizesis seems to be such that the backward loculus has time to make up the leeway and show a stage apparently similar to that of its companion. Naturally, the recovery from the contraction takes place earlier in the case of the one loculus than in that of the other and the previous condition in which visibly different stages occurred in the two loculi is restored.

The post-synizesic ("open" or "hollow") spireme stage.—Synizesis is followed by the "open" or "hollow" spireme condition, in which the strands representing the chromosomes, still connected by their ends with the nucleolus, expand from their contracted, clumped up condition and fill out the whole nuclear cavity. At this stage also it is perfectly certain that no continuous spireme is present. Median sections through the nucleus, happening to cut through the nucleolus also, place this matter beyond doubt (Fig. 12). The chromosomes are found to have undergone during the synizesis stage a great increase in their length, and when they are released from their contraction at the close of the synizesic period and stretch out, they not only fill out the nuclear cavity, but are, at any rate, in the case of the longer chromosomes, too long to be accommodated within the nuclear cavity in their fully stretched-out condition. They are, therefore, bent at a sharp angle where they come into contact with the nuclear membrane (Fig. 12) and may run along the inner surface of the latter for some distance and then turn inwards in the form of hooks. A large group of such long strands crossing and re-crossing and touching one another at various points creates the impression of a continuous spireme, the illusion being even stronger in nuclei which happen to have been cut tangentially, in which it is impossible to fully trace the course of each single strand (Fig. 13).

The changes observed in the nucleolus in the earliest post-synizesic stages are most remarkable. It is not only found to have undergone an increase in size and curious amoeboid changes of shape, but also to have developed sucker-like projections to which the chromosomes are attached, either directly, or indirectly through connecting-pieces of chromatin, or chromatin-like intensely staining material. Some of these changes of shape undergone by the nucleoli at this stage are shown in figs. 12 and 14, where the manner of attachment of the spireme-threads to the nucleolus is likewise to be seen. As the "hollow-spireme" stage advances, the sucker-like appendages are resorbed, and the nucleolus gradually returns to its normal shape (Figs. 15, 16). It is extremely probable, if indeed not certain that these changes in the nucleolus which are first observed in the earliest post-synizesic stage, must have been in existence during the whole of the synizesic period also, though shut out from view by the surrounding tangle of spireme threads. It is hardly possible that such extreme modifications in the nucleolus could suddenly jump into existence at the close of synizesis; moreover, the fact that the further changes observed in the nucleolus as the open spireme condition advances are all in the direction of *restoring* the nucleolus to its normal form and condition also point to the conclusion that these profound changes in that cell-organ, first *observed* at the commencement of the hollow spireme condition really go back to the synizesis stage itself, though shut out from our view.

In any case, it is quite clear that synizesis is a period of active growth for the chromosomes; it has been pointed out already that the spireme-threads when they come out of the " first contraction " have undergone a very considerable increase in length. In fact, it is not improbable that the chromosomes are at their maximum size at this stage in the whole course of the meiotic division. The material required for this growth is provided by, or more probably through the agency of, the nucleolus, which is in a state of great activity, and establishes a close connection with the chromosomes. The sucker-like projections provide not only better points of attachment to the spireme-threads, but may also act as channels for the transfer of material from the nucleolus to the chromosome. It is not possible however, that all this material comes from the substance of the nucleolus itself, as it would not be enough to account for the extensive growth made by the chromosomes; it is much more likely that the cytoplasm also makes a very considerable contribution. The increase in the size of the nuclear cavity and the ingress of cytoplasmic fluid during the early and middle stages of synizesis are significant in this connection. The nucleolus also makes its own contribution as shown

by its very pale,—almost whitish—color in the post-synaptic condition, but it is chiefly as an active agent which transforms the substances obtained from the cytoplasmic fluid, and elaborates them into material which the chromosomes could utilize for their growth, that the nucleolus seems to play its principal part in this connection.

Internal structure of the spireme-threads in the post synizesic stage.—The strands of the post-synizesic spireme are formed, beyond all doubt, by two filaments closely twisted round each other, so as to form a double spiral. In the entire (un-cut) condition, the spireme-thread appears like a single thick smooth strand in the early stages of the open spireme; but even at this stage, cut ends of the spireme-thread may show the twisted structure (Fig. 13). At later stages, however, when the spireme-thread becomes gradually untwisted, and the component filaments condense,—changes in connection with the formation of the pachytene, which are dealt with in greater detail below. the double spiral structure becomes extremely clear (Figs 15 and 16) since the thickened filaments form the loosely twisted arms of a long loop formed by each synaptic pair of chromosomes.

Changes in the post-synizesic spireme preparatory to the formation of the pachytene.—Correlated with the notion that the post-synizesic spireme is "continuous" is the idea that the further changes it undergoes are in the nature of a "break-down". As a matter of fact, however, the changes consist essentially in a process of condensation, involving the untwisting of the filaments composing the spireme-thread and a shortening and thickening of each of these filaments (Figs. 15-19). This contraction of the spireme-threads causes them to break their contact with one another as they become shorter and shorter, and the "spireme" becomes "broken down". Such an appearance may be still further emphasized in cut nuclei, in which it is impossible to fully trace the course of the strands which may happen to be cut.

During the advanced stages of the untwisting and condensation of the spireme-threads, the writer has noted appearances which recall F. A. Janssens' figures of the formation of "chiasmas" at the nodes of the double spiral, which are believed to be concerned in effecting mutual interchanges of sections of chromosomes resulting in a "recombination" of "genes" (Figs. 16, 17 a and b, and 18). The writer's attention was drawn to this matter during a recent re-examination of his slides, and he has, therefore, been unable to study the matter in detail; but he intends to discuss certain aspects of it on the basis of his preliminary observations in a later section of this paper.

Formation of the pachynema.—As stated above, the paired chromosomes of the late open spireme condition form long loops connected by their lower ends with the nucleolus, and with the arms, representing the individual chromosomes, loosely twisted round each other (Fig. 16). The untwisting begins in each thread of the spireme at the upper end and progresses downwards; the two filaments into which the thread is resolved, however, remain connected with each other by their distal ends. The untwisting and the condensation proceed till simple loops with two thick, rather curved arms (Fig. 19) are produced. In the case of the shorter chromosomes, the process is completed earlier than in the case of the longer ones. Gradually, the two arms become straightened out as they continue to contract and thicken and approach each other side-by-side (Fig. 20); finally, they come into contact, become intimately united and apparently fused together, forming the haploid number—fourteen—of short, thick intensely staining pachytene bodies (Figs. 21 and 22).

While there is thus a very well-marked pachytene stage in *Cyanotis* and a clear "pseudo-reduction" in its formation with all its implications concerning the nature of the synaptic union in this species, it is well to note that the process is not quite so simple as in the auxocytes of certain animals like *Tomopteris* or *Dendrocoelum*, to mention only a few familiar instances, where the synaptic chromosomes directly condense into the pachytene bodies. In *Cyanotis*, on the other hand, complications are introduced by the occurrence of the synizesic contraction as well as by the early twisting of the synaptic mates round each other with a corresponding untwisting during the condensation in the course of the formation of the pachytene. The writer will try to discuss the meaning of these differences in a later section of this paper.

The "thick bouquet" formed by the condensed chromosomes with the nucleolus at the base during the later stages of the pachytene (Fig. 21) resembles in a very striking manner the corresponding stage in animal auxocytes. The nucleolus at the base, forming an integral part of the "bouquet" is a perfectly constant feature, an examination of thousands of nuclei at this stage having failed to show a single instance where the condition of things was different.

Condition of the nuclear cavity in the pachytene stage.—The pachytene represents a state of extreme condensation not only for the chromosomes, but for the entire nucleus; for, in the advanced conditions of that stage the nuclear cavity is found to have undergone a very great contraction and to have become even smaller than it was in the leptonema stages (Figs. 19–22).

Passage from the pachytene to the diffuse stage.—As already stated in a previous section of this paper, a single slide shows these transitional conditions, which probably means that they are passed through with great rapidity. It is perfectly clear, however, that a diplonema stage does not follow upon the pachytene in this species as is so very commonly the case. The passage to the diffuse stage, on the other hand, is direct.

As a preparatory for passing into the diffuse stage the chromosomes which are in a state of extreme condensation begin now a process of de-condensation. Still attached to the nucleolus by one end, they elongate and their edges become jagged or bluntly toothed (Fig. 23); as the elongation continues, the indentations on the edges become removed further apart from one another and also assume a more and more rounded contour. The nuclear cavity enlarges (Figs. 22 and 24). By further elongation and de-condensation, long thick bodies with a very distinctive structure are formed, consisting of intensely staining narrow segments alternating with very lightly staining ones (Fig. 24). This peculiar structure gives these bodies a very characteristic transversely banded appearance. It is probable that the "chromomeres" have again come into view, being represented by the deeply staining segments; if such be really the case, each deeply staining segment must be presumed to be the product of the 'fusion' or union of two corresponding chromomeres on a homologous pair of chromosomes.

At this stage the chromosomes are found to have detached themselves from the nucleolus, the shorter ones first and then the longer ones, and to have distributed themselves in the nuclear cavity.

Diffuse stage.—The nucleus now enters upon a very well-marked diffuse stage. The transversely banded post-pachytene bodies contract and stain with steadily diminishing intensity. The lightly staining bands however de-stain more rapidly than the deeply staining ones, so that the structure now appears like a thick line broken at short regular intervals (Fig. 25). The deeply staining segments appear also to steadily diminish in size; finally, they completely lose their staining power and the nucleus has definitely reached the diffuse stage (Figs. 26, 27). At the extreme diffuse stage (Fig. 27), it is impossible to distinguish individual chromosomes among the contents of the nuclear cavity which stain a light brown with haematoxylin. The nucleolus, however, which stains an intense black is a very conspicuous object. The nuclear cavity is found to have undergone a very considerable contraction (Figs. 26, 27). The diffuse stage seems to last a good length of time, shorter however, than does the synizesic condition.

Post-diffuse stage, " the second contraction ".—When the nucleus recovers from the diffuse stage, it is observed that the nuclear cavity has undergone a remarkable enlargement. (Compare Figures 27 and 28). The diameter may show an increase of more than 50 per cent which means that the volume has increased four or five fold. The chromosomes now make their appearance as long slender filaments associated in pairs and twisted about each other in a loose and irregular manner, and sometimes with their upper portions diverging rather widely from each other (Fig. 28). They are once again seen to be connected by one end with the nucleolus which stains feebly and undergoes changes in shape comparable with, but perhaps not quite so extensive as those observed in the post-synizesic spireme (Fig. 30). The staining reaction of the chromosomes is at first feeble, but becomes more intense as the filaments contract and become shorter and thicker. The twist becomes tighter in the lower portions of the double strands, but remains loose above, and may be altogether wanting in the uppermost portions; the filaments are connected together by their upper ends so as to form loops. The nucleus has now entered upon a very distinctive stage long familiar under the name of " the second contraction " (Fig. 29). As they condense further, the chromosomes assume a peculiar granular look, and stain a deep *blue-black* (Fig. 31). By further condensation they lose the granular structure, become more solid, and change their staining reaction to a jet black. They become rod-shaped and are found disposed round the nucleolus in pairs. With further condensation they become short thick bodies, and members of each pair become intimately united with each other (Fig. 32). At this stage, it is observed that some of the bivalents are arranged round the nucleolus in two series or tiers one above the other, that is to say, one set of bivalents immediately in contact with the nucleolus and a few others forming a second series outside the first (Fig. 32). This behaviour appears with great regularity in every case. In all probability, it is brought about by the fact that during the late second contraction stage, some of the chromosome-pairs are connected with the nucleolus directly while others,—generally the short ones, are connected only indirectly, through the strands of another pair, to which they become attached. In this condition the nucleus enters upon what might be called the pre-diakinetic stage.

The pre-diakinetic stage.—This stage is in this species one of very great interest, because of the de-conjugation of the constituent members of the bivalents, and the consequent emergence of the *somatic* or *diploid* number of chromosomes, followed by a subsequent re-union on the diakinesis stage proper, resulting in the formation of gemini.

So far as the writer is aware, such a behaviour of the chromosomes in the pre-diakinetic stage, though made familiar on the zoological side by the work of Henking and that of Gross (on *Pyrrhocoris*), that of Rückert (on elasmobranchs), that of Agar (on the lung-fish *Lepidosiren*, *Quarterly Journal of Micr. Science LVII*) and that of Hogben (on gall-flies), has not yet been reported in the case of any plant, with the possible exception of *Oenothera*. The bivalents of the early pre-diakinetic stage, which are, as stated before, thick double bodies arranged round the nucleolus, generally in a single series, but in the case of some in two series, now undergo a process of de-conjugation. This is initiated by a slit between the two univalents (Fig. 32), followed by a separation of the two members of each pair, one retaining its position in connection with the nucleolus while the other by rotating through an angle of 180° in a plane parallel to its long axis assumes an end-to-end position with reference to the first (Fig. 33). In this condition of end-to-end union the univalents remain for some time, then separate from each other to a greater or less extent, and detaching themselves from the nucleolus, emerge into the nuclear cavity *as univalents* (Fig. 34). In the case of bivalents arranged in two series the de-conjugation proceeds in such manner that the four univalents derived by the splitting up of the two bivalents form a series of four rods placed end to end (Fig. 34).

The univalents do not remain separate for a long time but soon proceed to re-union. As a preparatory step, they come into contact with each other once again *end-to-end* ('telosyndesis') and the free ends of both approach till the two rod-shaped bodies are brought into a side-by-side position. At this stage, it is always possible to see a few pairs whose members are inclined towards each other at various angles, so that there can be no doubt as to the manner in which the side-by-side position is assumed.

The final pre-diakinetic phase of de-conjugation, and the re-assumption of the side-by-side position as a preparatory to re-union does not take place simultaneously in the case of all the bivalents but earlier in the case of some than in that of others, so that some are still in a paired condition and connected with the nucleolus, while those which have become separated very early and emerged into the nuclear cavity may have gone a long way towards assuming, or even finally taken up, a side-by-side position. There does not seem to be any very great regularity with regard to this matter (Fig. 34).

The situation in this case differs slightly with regard to details from that reported in *Lepidosiren* by Agar. According to this investigator, it is possible at certain stages of the pre-diakinetic

condition in *Lepidosiren* to see the full somatic (diploid) number of univalents lying in the nuclear cavity, which is not the case in *Cyanotis*. Apparently, the de-conjugation and the commencement of the re-union are separated in *Lepidosiren* by a good interval of time, while in *Cyanotis*, the early stages of the re-union follow closely upon the separation of the univalents. There is, however, no difference in principle between the two cases: the essential feature, namely, *the emergence of the chromosomes as univalents in the pre-diakinetic phase* is the same in both. Attention may also be drawn to the fact that while thus emerging, the members of each homologous pair are connected end-to-end.

Re-union and the formation of the gemini-diakinesis.—The univalents which have re-assumed a side-by-side position now join each other and become intimately united, so as to form the reduced number of more or less spherical gemini. Here again, the process is not simultaneous in all the pairs of chromosomes, and some may complete the union only when they are being shifted to the equator of the nucleus (Fig. 35).

Chromidia.—Just before the final stages of the diakinesis, i.e., during the formation of the gemini, there appears *within* the nuclear cavity, a fairly large irregularly shaped body with a rather granular structure, which stains a deep grey with iron-haematoxylin. (Fig. 35). As the nuclear membrane is dissolved at the end of the prophase, this body is cast out into the cytoplasm where it remains till the telophase of the heterotypic division, though steadily decreasing in size and staining less and less intensely. How, and exactly when, it finally disappears the writer has been unable to determine. This body probably belongs to that ill-defined class of cell-constituents known as chromidia.

The origin of the achromatic figure.—The achromatic figure as observed in preparations made from material fixed in the modified "Flemming" mentioned in an earlier part of this paper is wholly intranuclear in its origin, bipolar at all stages and never has the coarsely fibrous appearance seen in material fixed in mixtures rich in acetic acid. The spindle-figure is initiated by means of polar caps, though the manner of origin of these latter seems to be rather different from that described in somatic cells by Robyns, Sharp and others. During the last stages of the prophase, and especially at the stage when the gemini are being formed, the nuclear cavity becomes distinctly elongated, appearing oval in section. At the ends of the long axis are the poles of the future spindle. The process of elongation of the nuclear cavity is continued being greatest at the poles and a corresponding contraction takes place in the equatorial zone. As a

result of this polar elongation of the nuclear cavity, two conical pointed "polar caps" of hyaline material become demarcated at the poles, and the gemini become crowded together in the steadily contracting equatorial zone. As the component chromosomes of the gemini begin to separate, delicate "fibres" appear in the polar caps. The nucleolus has in the meantime been steadily diminishing in size and finally disappears at a slightly later stage, seeming to melt away by degrees. The nuclear membrane now breaks down at the equatorial region and the fibres gradually extend to this region from the polar caps. As the anaphase advances the nuclear membrane completely disappears, the apices of the polar caps move apart from each other, the number of fibres becomes larger and the zone of their spread at the equator of the spindle-figure is also correspondingly increased. Ultimately, late in the anaphase, not only does the spindle stretch through the whole length of the nuclear cavity, but the cell as a whole assumes an elongated form, as if under the action of a longitudinal internal stress, acting in opposite directions towards the two poles.

The manner of origin of the spindle-figure in somatic cells, initiated by means of "polar caps" is rather different, according to Robyns (*La Cellule*, 34). The nuclear cavity is said to contract at the future poles of the spindle-figure, and the "karyolymph" exuding through the retreating nuclear membrane at this region is stated to form the polar caps; in these the spindle-fibres first appear. The writer has examined a large number of nuclei at this stage, and has been unable to see a retreating nuclear membrane at the poles. His preparations show that the polar caps are bounded by the nuclear membrane till the latter breaks down. The facts that with the advance of the anaphase, the pointed apices of the polar caps move apart from each other, and that at later stages the pollen-mother-cell as a whole becomes elongated also suggest that some kind of internal pressure originating within the nuclear cavity is responsible for pushing out the nuclear membrane at the poles.

In any case, whether the polar caps are held to be derived from a polar elongation of the nuclear cavity or whether they are held to be formed out of "karyolymph" left behind by the retreating membrane of a contracting nucleus, the important fact is that they are in either case nuclear, and not cytoplasmic, in origin. An examination of a very large number of pollen-mother-cells at this stage has failed to show the writer a single spindle which was multipolar at any stage, or anything like an "invasion" of a perinuclear weft of fibres into the nuclear cavity. In this connection, it is instructive to compare material fixed with the modified "Flemming" mentioned above with that fixed in a

mixture much richer in its acetic acid content and poorer in osmic acid, as for instance the "Bonn" mixture, which was used, both cold and hot, by the writer in the case of two lots of anthers. In such material all the features usually attributed to the achromatic figure in microsporogenesis, such as a multipolar spindle in the earlier stages, a perinuclear zone of fibres, and a coarsely fibrous spindle at the later stages occur with unfailing regularity. These features find an even more exaggerated expression when the fixative is used hot, the spindle appearing as if cut by deep furrows along prominent fibres.

Metaphase, Anaphase and Telophase of the heterotypic division.—These stages present no special features and may, therefore, be very briefly dealt with. The division I is disjunctional. No tetrads are formed. The lumpy chromosomes of the metaphase (Fig. 39) become divided into univalents, and as the anaphase commences these move apart from each other and are only connected by a narrow neck. As the anaphase advances, the univalents become completely separated and move towards the poles (Fig. 40). In the telophase the chromosomes become densely aggregated at the poles and proceed towards a reconstruction of the daughter-nuclei (Figs. 41, 42). A transitory cell-plate is laid down. Before the telophase-groups of chromosomes have proceeded far towards the reconstruction of the daughter-nuclei, division II commences and the reconstruction is interrupted.

Division II.—This also presents no special features. The quartet-formation is by means of furrowing and is of the bilateral type (Figs. 43, 44).

IV. Discussion.

Among the many problems with a theoretical bearing, connected with meiosis, two are specially important in view of the part played by the chromosomes in heredity. These refer to the nature of the synaptic union and the precise manner in which such union is brought about. The first of these questions is doubtless the more important of the two, but the second has so far received greater attention at the hands of cytologists. To these two questions the writer proposes to devote the greater part of this section of the paper. There are many other problems of less importance on which different views have been put forward, and these the writer proposes to review in the briefest possible manner in dealing with the changes observed in *Cyanotis* in the course of meiosis stage by stage.

1. *Origin of the leptonema threads.*—It is clear that the chromocentres are formed by a condensation of the material from the reticulum and that they are not structures that persist from the pre-meiotic telophase into the meiotic prophase. Each chromocentre

does not necessarily represent a single chromosome, since more leptotene threads than one may take their origin from a single chromocentre. In conformity with this fact is also the fact that the number of chromocentres is smaller than the diploid number of chromosomes characteristic of the species (i.e., 28).

2. *Polarization of the leptotene threads.*—It is well-known that in the case of many animals, the leptotene threads, bent into loops are oriented in such a manner that their ends are directed towards the centrosome which lies in the cytoplasm just outside the nuclear membrane. It is generally believed that the central bodies play an important part in bringing about the side-by-side conjugation of the leptotene threads (See Wilson, E. B. *The Cell in Development and Heredity*, 3rd Ed., p. 567). In *Cyanotis*, as stated in the descriptive part of this paper, the leptotene threads become likewise "polarized" in a clear and unmistakable manner, but with reference to the *nucleolus* (plasmosome). Not only do the ends of the leptotene threads become directed towards the nucleolus, but they become actually connected with it. This feature appears with such a persistent regularity in the tens of thousands of nuclei in the early and middle prophasic stages which the writer has examined, that it would be an untenable position to maintain that this close association between the nucleolus and the chromosomes is merely casual and without any significance. Nor does the writer think it likely that this behaviour is peculiar to *Cyanotis*; an extensive examination of published figures shows that a more or less intimate connection between the nucleolus and the "spireme" during the early prophase is a phenomenon of wide-spread occurrence in plants, being especially conspicuous during synizesis when the nucleolus may even be completely enclosed within the knot formed during "the first contraction". The writer's observations in this connection are also confirmed by two recent papers,* one on meiosis in *Lathyrus* (Latter, J., in *Ann. Bot.* 40) and the other on meiosis in *Ranunculus* (Sorokin, H., in *Amer. Jour. Bot.* 14 (2). Both these investigators are agreed that the nucleolus is in a state of great activity in the early prophase; the shifting of its position towards the nuclear membrane, the amoeboid changes of shape undergone by it, the "budding" by which is probably meant what the writer has called the formation of sucker-like protuberances have likewise been observed as a constant feature; establishment of a connection between the spireme and the nucleolus is also confirmed, though on this point, the observations differ with regard to details. The writer is inclined to think that a more detailed study of the

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* The writer has seen only summaries in the *Biological Abstracts*.

meiotic prophase in future may show these phenomena, including the early "polarization" of the leptonema threads with reference to the nucleolus to be of wide-spread occurrence.

Assuming this to be the case, the situation may be explained in two different ways; either the centrosome has been completely lost in the higher plants, and the nucleolus has taken over the functions performed by that structure during the meiotic prophase in organisms that possess it such as animals generally, or the lower plants; or that the centrosome substance, whatever its nature, has in the higher plants become in some manner "associated" with the nucleolus. The writer proposes to discuss this matter more fully in connection with his observations on the origin of the achromatic figure.

3. *The manner in which synaptic union is brought about.*—On the zoological side, the parasynaptic interpretation of meiosis, originally put forward by H. de Winiwarter, and based on his work on gametogenesis in mammals, may be said to have found a very general, though, perhaps not universal acceptance. This has been due to the work on a great variety of animals by a number of later investigators, among whom may be mentioned A, and K. E. Schreiner (on *Tomopteris* and other annelids), F. A. Janssens (on salamanders), E. B. Wilson (on hemipters), D. H. Wenrich (on grasshoppers), J. Gelei (on platodes) and W. E. Agar (on the lung-fish *Lepidosiren* and on the marsupials). On the botanical side, while the parasynaptic interpretation has received strong support by the work V. Gregoire (*Lilium*, *Osmunda*, etc.), J. Berghs (on *Allium*, *Drosera*, etc.), C. E. Allen (on *Lilium*, *Coloeochaete*), K. Miyake (on *Lilium*, *Allium*, *Tradescantia*, etc.), E. Strasburger (on *Lilium*, etc.) and Yamanouchi (on *Polysiphonia*. *Osmunda*, *Nephrodium*), to mention only a few workers, the telosynaptic theory also finds a good deal of support. Among its advocates are J. B. Farmer and J. E. S. Moore (on *Lilium*, *Osmunda*, *Psilotum*); D. M. Mottier (on *Lilium*, *Allium* and *Tradescantia*); L. Digby (on *Primula* and *Osmunda*); and R. R. Gates (on *Lactuca* and *Oenothera*). A curious circumstance in this connection is the fact that in the case of a number of plants (*Lilium*, *Osmunda*, *Tradescantia*, *Allium*, *Galtonia*, etc.,) the two opposing interpretations have been put forward in the *same* object by different observers. But as it is most improbable, if indeed, not impossible, that a process of such fundamental importance as synaptic union would be so irregular in its course as to take place sometimes in one way and sometimes in another and a very different way in the same plant, one is forced to the conclusion that an explanation for the difference of opinion must be sought elsewhere than in a difference in the actual condition of things. As E. B. Wilson remarks, (*The Cell in Development and Heredity*, p. 565

of the 3rd Edition) " Some of the existing divergence of interpretation has, no doubt, arisen from errors of observation in this difficult field. To the writer, however, it seems probable that the divergence may also be due in part to a failure to reckon with all the cytological phenomena and in particular with possible secondary modifications ".

Apart from the evidence derived from direct observation under the microscope, which, however, has always been easy to assail on account of the acknowledged difficulties connected with microscopic observation during the early prophase stages, the parasynaptic interpretation is supported by a large body of indirect evidence of a very convincing character. (See review by E. B. Wilson, "*The Cell*", 3rd Ed., Chapter VI). It is enough to consider here the "pseudo-reduction" observed in the formation of the pachytene bodies. This phenomenon can have only one meaning and that is that the synaptic union is completed in the early and middle stages of the prophase and is not deferred until the "*looping*" in the "second contraction" or the slightly later diakinetic stage. In the case of many animals, where the synaptic pairs of chromosomes directly condense into the pachytene without any twisting occurring between the members and without the interposition of a synizesic contraction, the evidence supplied by the phenomenon of "pseudo-reduction" in support of parasynapsis amounts to a demonstration. But even in cases like that of *Cyanotis* where certain complications are introduced by the twisting of the synaptic mates and by the interposition of the "first contraction", the production of the reduced number of pachytene bodies clearly shows that the synaptic union has been completed, and is not deferred till the final stages of the prophase, as would be the case if the telosynaptic interpretation were applicable.

Attempts have been made by supporters of the telosynaptic theory to show that the doubleness seen in the early prophasic "spireme-threads" is due to a re-association of the split-halves of single chromosomes and not due to a synaptic pairing of homologous chromosomes. It has been claimed that such "doubleness" is visible as early as in the last pre-meiotic telophase: it is argued if this duality were really due to synaptic union, it should first appear only in the meiotic prophase and not earlier. Apart from the acknowledged inadequacy of the evidence to prove a telophasic splitting of the chromosomes even in somatic mitosis, cases like that of *Cyanotis* where the leptotene threads take their origin from chromocentres which are clearly derived from a condensation of the nuclear reticulum in the early prophase, effectively dispose of the argument in support of telosynapsis based upon the splitting of chromosomes in the pre-meiotic telophase.

The principal piece of evidence in support of telosynapsis rests upon the peculiar behaviour of the chromosomes in the course of their emergence from the second contraction, and preparatory to the diakinetic stage in certain animals and plants of which it is enough to consider here the case of *Oenothera* species, which have been subjected to a painstaking and thorough research by R. R. Gates, R. E. Cleland and others. The chromosomes, in the course of their emergence in the pre-diakinetic stage, appear in the somatic, i.e., diploid number, and connected end-to-end so as to form chains, rings, etc., of different types characteristic for each species. The emergence of the *diploid* number of chromosomes at this stage is interpreted to mean that synaptic union has not occurred until this stage; the fact that the members of each pair of homologous chromosomes are linked end-to-end is interpreted to mean that the synaptic union is primarily end-to-end (telosynapsis), although it may secondarily become a side-to-side union. Synapsis is, therefore, considered to be deferred until a very late stage, almost the end, of the prophase.

This line of argument, based as it is on facts which must be admitted to be incontrovertible, would have been unanswerable, if it had not overlooked the possibility that the bivalent chromosomes might have become secondarily disjoined in the pre-diakinesis stage after a previous synaptic union early in the prophase. The writer would once again refer to the extract, already quoted, from Wilson. In continuation of this passage, Wilson says: "Interesting possibilities in this direction are suggested by the phenomena of diakinetic de-conjugation and reunion". The peculiar behaviour of the chromosomes in the pre-diakinetic stage in *Cyanotis*, already dealt with in detail in the descriptive part of this paper, also strongly suggests that the situation in *Oenothera* is probably to be interpreted in the manner pointed out by Wilson. There is, in *Cyanotis*, an extremely clear case of parasynaptic union early in the prophase resulting in the formation of the *reduced* number of pachytene bodies, and an equally clear post-synaptic de-conjugation which can be traced step-by-step in the stages preceding diakinesis resulting in the emergence of the diploid number of chromosomes, the members of each homologous pair being placed *end-to-end* in the course of such emergence as in *Oenothera*. The emergence of univalents towards the end of the prophase in any particular case does not, therefore, necessarily prove that a previous synaptic union has not taken place. We are in all probability dealing in such cases with what Wilson has aptly termed "secondary modifications" the meaning of which is not yet known.

In this connection, one must not overlook the fact that from time to time papers have appeared which describe in a circumstantial

manner a parasynaptic mode of union in the early prophase even in species of *Oenothera*. One of the latest of such papers, for instance, is by Y. Sinoto (*Microsporogenesis in* Oenothera sinuata, *Bot. Mag. Tokyo*, 41 (483)).* This circumstance makes it all the more probable that the peculiar behaviour of chromosomes observed in the course of their emergence from the "second contraction" in *Oenothera* belongs to the class of diakinetic disjunctional and synaptic phenomena, with an unknown significance, which do not exclude the possibility of a previous side-by-side union.

4. *The zygonema, synizesis and pachynema stages; the nature of the synaptic union.*—This question is one of very great theoretical importance, since upon its solution depends the correct interpretation from the cytological point of view of the phenomena of linkage which play such an important part in heredity. The principal views held with regard to the nature of the synaptic union may be summarized as follows:

(*a*) the synaptic mates become completely fused;

(*b*) however intimate their association may be, the synaptic mates do not become fused together: this association consists in a close side-by-side approximation of the homologous chromosomes;

(*c*) the synaptic mates do not become fused together, but remain distinct and twist round each other so as to form a double spiral.

(*a*) With regard to the first of the above views, the synaptic mates are considered to become fused together so as to form a "mixochromosome" represented by the pachytene thread. The implications of such a view are far-reaching. It means that the synaptic mates lose their individuality in the course of the union and that the univalents emerging out of such a union would be structurally different from those that entered into it, at all events if the separation were in a plane different from that of the union. Such a view of the synaptic union has really not much to support it beyond the fact that at certain stages the union is so intimate that the mates become indistinguishable. But, "several careful observers have reported that the doubleness is visible at all stages in properly fixed preparations" (L. W. Sharp), and undue importance should, therefore, not be attached to what might seem like a complete fusion in particular cases.

The evidence from experimental genetics is also against this view. For instance, in cases of recombination, it is clear that while the chromosomes have mutually interchanged definite segments or sections,

* The writer has seen only a summary of this paper in the *Biological Abstracts*. See also R. R. Gates in *Bibliogr. Genetica*, IV, p. 401 ff.

the "genes" within each of these sections have remained undisturbed. There is no reason why this should be so if the chromosomes have become completely fused in synapsis and the product of such fusion is subsequently re-partitioned. As a matter of fact, the view that synaptic union results in a complete fusion of the mates, involving the loss of their identity has but few supporters to-day.

(*b*) This view is widely represented in the zoological literature; synapsis involving merely a close side-by-side approximation, accordingly, may be a mode of union of widespread occurrence among animals.

(*c*) That the leptotene threads twist round each other during the synaptic union has been reported, both in the case of plants and in that of animals by many observers (for instance, Gregoire in *Osmunda* and *Allium*, Agar in *Lepidosiren*, Lee in *Helix*, Janssens in *Batracoseps*). But E. B. Wilson considers the evidence in support of such torsion as "very inadequate." (*The Cell in Development and Heredity*, 3rd Ed., p. 555). T. H. Morgan considers that "this interpretation is often open to suspicion. It is extremely difficult, in fact, to determine when threads as delicate as these come into contact with each other whether they pass above or below, i.e., above at one node and below at the next" (*Silliman Memorial Lectures* : "*The Theory of the Gene*," 1926, p. 43). That there is some justification for this criticism cannot be denied. In *Cyanotis*, however, the writer believes that there is an extremely clear case of synaptic twisting; and one does not need, in this case, to rely solely on observations made in the leptotene stage. As described in detail in an earlier part of this paper, there is an extremely clear *untwisting*, in progressive stages, during the post-synizesic condition (see Figs. 15–17); and as the filaments at this stage are also condensing and becoming thicker, they are no longer "delicate" (in fact, they may be observed in the clearest detail and without the least trouble with a 4 mm. dry objective) and observations made upon them can no longer be said to be "open to suspicion". As post-synizesic untwisting can have no meaning unless there has been a previous twisting, these observations may be safely taken as confirming those made in the leptotene stages with regard to the twisting of the synaptic mates.

Concerning the nature of the processes which bring about a twisting of the leptotene threads round each other, the writer is unable to offer anything like a complete explanation ; some of the facts observed in this connection, however, are suggestive. For instance, the twisting starts at the basal, i.e., nucleolar, end of the double strand and progresses upwards ; it is loose at first and becomes progressively tighter. These facts probably mean that the twisting is brought about by a

rotation of the free ends of the filaments in opposite directions,—movements comparable to the 'nutations' executed by the sensitive tip of the shoot of a climbing plant.

As already stated in the descriptive part of this paper, as the zygotene stage advances and the twist between the chromosomes becomes tighter, the double strand becomes stiff and erect, to all appearance as a consequence of the twisting. Indeed, it is not improbable that the "first contraction" itself is, at least in some measure, due to the torsion. An analogy with the stiffening of a double strand of thread when twisted tightly, or the folding together and the formation of a 'knot' when each member of a group of such double strands fixed to one point is subjected to a like process can at best be but crude, yet may help us to visualize the processes which may occur at these stages.

Not much need be said here concerning the significance of the prophasic twisting of the chromosomes in bringing about "crossing-over". (See papers by F. A. Janssens in *La Cellule* dealing with the cytological aspects of the matter, and various publications by T. H. Morgan and his fellow-workers, dealing with the matter from the point of view of genetics). It is obvious that if this torsion is followed by a simple un-twisting, *i.e.*, a mere reversal of the twisting process, no crossing-over can result. Some kind of fusion at the nodes, and a separation in a plane different from that of the union would be necessary. The writer has already pointed out that certain appearances during the *late* stages of untwisting and condensation of the post-synizesic spireme threads suggest that such a separation in a new plane (following a previous fusion) at the nodes may occur. For instance, in Fig. 17 (*a*) at the nodes marked *n* and *nn* the filaments, which are now in a fairly advanced stage of condensation, appear to be fused together, and to be in the same plane, *i.e.*, neither of them passing above or below the other; in the later stages of condensation, just previous to the formation of the pachytene loops, represented by Fig. 17 (*b*) where the possibility of any deception, due to the slenderness of the structures being examined is excluded, it is clear that the two arms of the double chromosome lie in the same plane: the lozenge-shaped slits seem to initiate the separation in the new plane, *i.e.*, to the right and the left. As far as the writer's present studies show, while it is very probable that the *fusion* at the nodes takes place when the threads are yet thin, the *final separation* in the new plane occurs when the threads are in a *condensed* condition, in fact, just previous to the formation of the pachytene loops. The arms of the pachytene loops would then have to be considered as representing chromosomes which have already undergone the mutual

segmental interchange. The writer is studying the matter in greater detail, but has thought it desirable to publish these preliminary observations for what they are worth.

5. *The post-pachytene stage.*—In the course of the changes which follow the pachytene, the chromomeres apparently once again come into view, as the condensed pachytene bodies undergo a decondensation and becomes elongated. They must now be regarded, however, as "double" chromomeres, resulting by the fusion of corresponding pairs and not as single bodies. Why the chromomeres should pass out of view during the late leptonema, and again come into view in the post-pachytene stages, the writer is unable to explain.

6. *The diffuse stage*, which clearly results by a progressive loss in the staining capacity of the post-pachytene bodies, is in all probability, as much a stage of growth in this case as it is very generally held to be in the case of animal auxocytes.

The post-diffuse stages, which for the sake of convenience, may be divided into early and late "second contraction" stages, and in which the chromosomes are once again found to be twisted round each other, *can* provide further opportunities for "crossing-over" to take place, but there is absolutely nothing to suggest that this does actually happen.

During the early second contraction stage, the nucleolus is found to have undergone changes comparable to those in the "first contraction", though perhaps not quite so extensive. This fact suggests that the second contraction may be an extension of the growth stage, continuous with that in the diffuse condition.

The clear omission, in Cyanotis, of a diplotene stage, in which "crossing-over" is generally believed to occur, is perhaps not without significance. The ample opportunities provided during the earlier stages of the prophase for this phenomenon to occur, may render a diplonema stage superfluous.

The final stages of the "second contraction" have been dealt with in some detail in the descriptive part of this paper under the name of the "pre-diakinetic stage". One further aspect of this matter which would have been rather out of place on the previous occasion on which this matter was dealt with, may be mentioned here. The phenomena of diakinetic de-conjugation and re-union must be of a fairly wide-spread occurrence, since they are observed in such diverse organisms as fishes, gall-flies and at least one angiosperm, neglecting for the present the possible case of the Oenotheras. As such, they cannot possibly represent an anomalous or aberrant condition, but must have some meaning and serve some definite purpose.

7. *The origin of the achromatic figure.*—That the appearance presented by the achromatic figure in pollen-mother-cells in material fixed in mixtures rich in acetic acid represents in a great measure distorted artifacts seems to be beyond doubt. Devisé (*La Cellule*, 32) by a careful study of material from *Larix*, fixed according to the mitochondrial technique of Benda, which admittedly gives a much finer fixation, especially of the non-chromatinic elements of the cell than the methods previously employed, has shown that the achromatic figure is bipolar at all stages, and intranuclear in its origin ; he has also demonstrated that the "weft of fibres" generally reported to be formed in the cytoplasm in the perinuclear region and believed to initiate the spindle-figure by "invading" into the nuclear cavity, as well as the coarsely fibrous appearance presented by the spindle-figure itself, are artifacts. The few observations which have been made on living material by Chambers and Sands and others, also show that the coarsely fibrous appearance of the spindle is not natural. The conclusions to be drawn from the results of the writer's study on *Cyanotis* in this respect, set forth in detail in the descriptive part are in general similar to those of Devisé, though differing in the matter of details, which is not surprising, considering the difference in technique.

The origin of the anastral type of the achromatic figure, specially as it occurs in the higher plants is a question with regard to which not much is known. That it is a secondary type, derived from the amphiastral type, as it clearly is in the case of the oöcytes of certain animals, appears to be certain. In the thallophytes centrosomes generally occur and take part in cell-division. Among the bryophytes, pteridophytes and gymnosperms with motile spermatozoids (the Cycadales and the Gingkoales) centrosomes regularly appear in the course of spermatogenesis; they may do so at fairly early stages in the spematogenous tissue, in which case they take part in cell-division or their first appearance may be deferred till various later stages, until in some forms they first appear in the spermatids themselves, as blepharoplasts, and then take part only in the formation of the locomotor apparatus of the spermatozoids. And in the case of at least one liverwort, which is of exceptional interest, that of *Preissia quadrata*, according to M. Graham centrosomes occur in the somatic cells also. In other bryophytes, pteridophytes and gymnosperms belonging to the groups mentioned above, although the cells in the somatic tissues have no centrosomes, the power to produce them when necessary is nevertheless retained. Among the angiosperms, of course, no centrosomes occur at any stage, though the earlier literature contains observations recording their existence, which however, have since been proved to be erroneous. It is clear, therefore, that with the

cessation of the production of *motile* sperms, the appearance of centrosomes at any stage in the life-history also likewise ceases. As Wilson says: "it seems reasonable, accordingly, to assume that the presence of asters and blepharoplasts in the gamete forming divisions represents the primitive amphiastral mode of miotosis that still exists in many thallophytes and has persisted in the sperm producing divisions because of a specific physiological motive." (Wilson, E. B., *The Cell in Development and Heredity*, 3rd Ed., p. 156). These considerations also make it evident that the higher plants have "lost" the central apparatus only secondarily and in a limited sense, and that this loss is connected with the formation of non-motile male generative cells.

Strasburger thought that in the production of the achromatic figure in the course of cell-division in the higher plants, the nucleolus, which he regarded as a store of "fibrillar" *kinoplasm*, specially concerned with the motor work of the cell, played a very important part. Phylogenetic considerations make it probable that this view is correct. Among the flagellates where generalized types of nuclei known as karyosome-nuclei occur, in which the chromatinic and nucleolar elements of the cell are still in the course of differentiation and separation from each other, and a specially differentiated central apparatus may or may not occur, the nucleolar element appears to give rise to what corresponds to the achromatic figure. In the more primitive forms, where the karyosome may form the chromosomes or bodies corresponding to them, the 'spindle' is formed out of the material left behind *after* the chromosomes are formed, which is presumably nucleolar in its nature. In more advanced forms, where a clearer differentiation occurs, and a central region corresponding to the nucleolus and a peripheral region corresponding to the 'reticulum' of the higher plants are marked off from each other (the chromosomes originating entirely in the peripheral region), the part played by the nucleolus in the formation of the spindle-figure is clearer; it generally elongates to form deeply staining polar caps, with which the groups of the daughter-chromosomes become associated. In the euglenoid flagellates, for instance, where in some forms centrioles are absent (*Euglena*) and present in others (*e.g.* in *Astasia* according to Bělař), the chromosomes are entirely formed out of the peripheral region, and the spindle is formed by the central (nucleolar) body, which plays the part of a "combined nucleolus and centrosome" ("nucleolo-centrosome"); where centrioles occur, these may be differentiated *within* this central nucleolar body (as for instance in *Astasia*). More interesting still from the point of view of the botanist is the situation in many green algae. In these, the nucleus while still primitive in its type

is more advanced in its organisation and the separation of the different nuclear elements has proceeded farther, so that it can no longer be open to reasonable doubt that the nucleolar bodies and the peripheral chromatinic region correspond respectively to the nucleolus and the "reticulum" of the nuclei of the higher plants. (See F. Oltmanns, *Morph. u. Biol. d. Algen*, 2 te Aufl., III, S. 14–18). In *Cladophora glomerata*, for instance, where nuclear organisation of this type occurs, it has been established by the work of Němec and T'Serclaes that the behaviour of the chromosomes conforms closely to that in the higher plants both with regard to manner of origin and division. When the spindle-figure ("Kernspindel") is being formed, the smaller nucleolar bodies disappear as does the nucleolus in the higher plants; but the main nucleolar mass ("Hauptnucleolus") bodily divides into two, like a karyosome, and each half becomes associated with a group of the daughter-chromosomes; no centrosomes are specially differentiated. In other related algae (as e.g., *Rhizoclonium*) however, the whole of the nucleolar material disappears when the spindle is being formed as in the case of the higher plants. Facts such as these when considered along with the known behaviour of the nucleolus in the course of cell-division in the higher plants where it disappears, or becomes unrecognizable as such just so long as a spindle-figure occurs in the cell make it probable that Strasburger's views mentioned above are substantially correct.

As to how the elimination of structurally differentiated centrosomes in the higher plants, with the retention of the power in the case of certain groups to differentiate them anew in connection with spermatogenesis has been effected, one can offer at present no more than speculative explanations. The writer's belief is that the centrosome represents no more than a special differentiation of the "fibrillar kinoplasm" of which the nucleus contains a store in the nucleolus, and which has, for reasons which may be connected with cytokinesis, the formation of locomotor structures and the like become more or less permanently located in the cytoplasm. Centrosomes differentiated *de novo*, as for instance, in the course of gametogenesis will then have to be regarded as derived from the nucleolar store of "kinoplasm". Support for this position is to be found among the protista, where the centrosomes are either characteristically intra-nuclear in position and sometimes formed *within* the karyosome, or where extra-nuclear in their position, often connected by means of a strand (centronema, rhizoplast) with the central (nucleolar) region of the karyosome-nucleus; in many protista, it is definitely known that such extra-nuclear centrioles, or their equivalents are intra-nuclear in their origin. Where no centrosomes are differentiated, those elements of

the karyosome left behind after that structure has made its contribution, if any, towards the formation of the chromosomes originate what corresponds to the spindle-figure ; as stated already, these elements are probably of a nucleolar nature (see the views of Berghs, Svedelius, and Neuenstein cited in Oltmanns, *l. c.*). The condition in *Cladophora* appears to be intermediate between the purely " karyosomal " condition found in the flagellates and that occurring, for instance, in *Rhizoclonium*, which, as pointed out already, bears a striking resemblance to the condition occurring in the higher plants. In such cases, the nucleolar material is often said to behave "like a combined nucleolus and centrosome" (*nucleolocentrosome*). But in the absence of evidence to show that these elements originally separate, have become "combined", this assumption, in the writer's view, introduces an unnecessary complication, really not required, or even warranted by the facts of the case ; it would be equally correct and simpler to say that in such cases centrosomes are "not differentiated" out of the nucleolar material instead of saying that the two elements have become "combined".

Instances where centrosomes are clearly formed *de novo* likewise point to the nuclear origin of these bodies. In the liverwort *Marchantia*, according to Ikeno, the centrosome comes out of the nucleus before each spermatogenous division, and dividing, takes part in the following cell-division. Yatsu reports that the artificial formation of cytasters in enucleate egg-fragments of the nemertine *Cerebratulus* is not possible unless such fragments have received material from the nucleus by a previous break-down of the germinal vesicle. It is probable that in these cases the centrosomes have their origin in *nucleolar* matter, considering that the nucleolar and centrosomal elements are closely "associated" (identical ?) in the nucleolo-centrosome of the lower organisms. In the case of the higher plants, with the cessation of the production of motile gametes and the adoption of the mode of cell-division by means of cell-plates rather than by constriction, the need for differentiating centrosomes at any stage of the life-history may also have ceased.

If the views stated above are correct, "the polar caps" of the higher plants have to be regarded as being essentially similar to those formed in the lower organisms considered before, which possess a nucleolo-centrosome and in which neither centrioles nor asters are differentiated. Wilson thinks that "the possibility remains that although true asters seem to have disappeared in the higher plants, central bodies, may still be present, perhaps very small, so as to have been overlooked, or intra-nuclear in position as is the case in some protista"; but it does not seem likely to the present writer that

centrioles are really differentiated in them. The melting away of the nucleolus during the late stages of the prophase and the polar elongation of the nuclear cavity rather suggests the flow of some fluid substance formed out of the nucleolus towards the poles which gives rise to the polar caps; the situation may be analogous to that in certain ciliates (as for instance in *Paramaecium* according to Calkins and Cull). The polar caps have then to be considered as masses of "kinoplasm" in an active condition. In this connection certain observations of Nassanov concerning the behaviour of the chondriosomes at the stage when the polar caps are formed in the course of mitotic division in the angiosperms are of great interest; he finds that they are oriented with reference to the polar caps in the same manner in which they are oriented towards the centrosomes in the case of many animals (insects, etc.) (Nassanov, D. N. in *Arch. Russ. Anat. Phys.* II). *

In speaking of the "polarization" of the leptonema threads with reference to the nucleolus in Cyanotis, the writer has indicated that this behaviour, recalling the orientation of the leptotene loops towards the centrosome in animal cells suggested either a replacement in the case of the higher plants, of the central apparatus with regard to some of its functions in connection with meiosis by the nucleolus, or alternatively an "association" of the centrosomal and nucleolar elements. In the light of the observations just made in connection with the origin of the achromatic figure, the second of these alternatives is the more probable one. And with regard to the nature of the "association" itself, the writer has already stated that in his belief the case is rather one of a "non-differentiation" of centrosomes from the general "kinoplasmic" store contained in the nucleolar material than a "combination" of two distinct and originally separate elements.

The writer has described in some detail the behaviour of the nucleolus in the early and middle prophasic stages, and it is necessary to recall here the main features of this behaviour. The nucleolus begins its activities by moving towards a side of the nuclear cavity and assuming a position as close as possible to the nuclear membrane, and becoming indeed often closely pressed against the latter. The alterations in its size and form, and the variations in the intensity of its staining reaction at the different stages have also been pointed out. The conclusions to be drawn from these observations have likewise been indicated, namely, that the nucleolus plays a very important part

* The writer has not seen this paper in the original, but only a reference to it in Wilson's *The Cell*, 3rd Ed., p. 163.

as an intermediary between the chromatinic and cytoplasmic elements of the cell, and that in this capacity it elaborates and provides the material required for the growth of the chromosomes. The position assumed by the nucleolus, close to, or in contact with, the nuclear membrane,—a position of the closest approximation to the cytoplasm which it is possible for an intra-nuclear body to occupy, is evidently connected with these activities of that cell-organ. The orientation of the leptotene threads towards the centrosome in forms which possess one is probably to be interpreted to mean as an orientation towards the kinoplasmic differentiation located in the cytoplasm itself.

The part played by the nucleolus in bringing about the twisting of the leptotene threads round each other, considered from the purely mechanical point of view, by fixing them at one end, is obvious.

One further aspect of the close connection which is established during the meiotic prophase between the chromatinic and nucleolar elements of the nucleus may be briefly mentioned here. In the higher organisms, an advanced degree of separation between these two elements has been attained, which is maintained during the normal metabolic activities of the nucleus. But when the nucleus passes into a specially active condition during the karyokinetic process, a close association between the two elements cannot yet be dispensed with, especially in connection with interactions between the chromatinic structures and the cytoplasm ; this association recalls to the mind the closer primitive association of the nucleolar and chromatinic elements in the karyosome nucleus.

V. General Conclusions.

A few general conclusions based upon the foregoing study may be appended here.

1. The most striking thing about the meiotic process as it occurs in *Cyanotis*, which may possibly be typical, so far as essentials are concerned, of the higher plants generally, is the great resemblance it bears to the process as it occurs among the animals. Some of the differences, such as the absence of a diplonema stage, are, as has been pointed out already, just those which may be expected to occur.

2. In certain respects, the meiotic process, as it occurs in the higher plants is a little more complicated than it is in the case of animals, especially in the early and middle prophasic stages, and its study, consequently is more difficult. A good deal of the divergence of opinion which exists with regard to the nature of the prophasic changes, often in the case of the same object is probably to be attributed to this circumstance. The writer's belief, based on his experience in the case

of *Cyanotis* is that even a tolerably satisfactory study of meiosis in the higher plants cannot be made in fixed preparations unless several hundred anthers, killed at various hours of the day are used for study.

3. It appears to be likely that synaptic union characterized by the formation of the "first-contraction" knot, which is of a very general occurrence among plants, and is also known to occur in many animals, and which seems to constitute a distinct type, is likewise characterized by a torsion of the leptotene threads; if this really proves to be the case, the higher plants may provide very suitable objects for the study of the cytological basis of linkage and recombination phenomena.

4. The nucleolus deserves a much more intensive study than has hitherto been made. Although few workers have agreed with Haecker in regarding the nucleolus as a "useless by-product", the general tendency has, nevertheless, been to consider that body as not of much consequence. The present writer believes that a closer study of this very definite and important cell-organ may throw a flood of light on some of the most fundamental problems of cell-organization.

5. The diakinetic synaptic phenomena may prove to be of a wider occurrence than now suspected, if a careful study of the mode of emergence of the chromosomes from the "second contraction" is made in every case. In any event, their meaning is yet unknown, and a wider study in a variety of forms may throw some light on their significance.

VI. Acknowledgements.

The writer's grateful thanks are due to his former professor at the Presidency College, Madras, Principal P. F. Fyson, and to Prof. M. O. P. Iyengar in whose sympathetic interest in his work the writer has found a source of great encouragement. His gratitude is likewise due to Dr. T. Ekambaram, also his former professor, who, in his capacity as President of the Board of Studies in Botany in the University of Madras has rendered the writer invaluable assistance by making it possible for him to get books and journals from the library of that institution at his place of work. Thanks in this connexion are also due to Mr. S. R. Ranganatham, librarian to the University for his unfailing courtesy.

Extracts from published works have been acknowledged in the appropriate places. Apart from these, the writer's indebtedness to Prof. Wilson's classical work, *The Cell in Development and Heredity*, and Prof. Sharp's admirable *Introduction to Cytology* has been great and he desires to acknowledge this fact with gratitude.

VII. Summary.

Microsporogenesis was studied in *Cyanotis cristata* in material fixed in a modified "Flemming" richer than the usual mixtures in its osmic acid content, and with the acetic acid content much reduced.

The leptotene threads originating from chromocentres which are derived ultimately by a condensation of the nuclear reticulum, form loops which become "polarized" with reference to the nucleolus ("thin bouquet") and connected with it; the nucleolus is found to have shifted its position towards a side of the nuclear cavity and often become closely pressed against the nuclear membrane. No continuous spireme appears to be formed at any stage.

Parasynapsis follows and the leptotene threads twist round each other in pairs, the double strands becoming stiff and erect with the progress in the torsion. The synizesic contraction follows, the twist between the chromosomes probably playing an important part in bringing about the contraction. When the chromosomes are released from the contraction, they are found to have undergone an extensive growth, the nucleolus playing a most important part in obtaining from the cytoplasm and providing the chromosomes with the material required for this growth; it is found to have undergone changes in staining reaction and remarkable amoeboid changes of shape, forming sucker-like protuberances to which the chromosomes become attached. The double chromosomes, forming long loops now undergo a process of untwisting, and observations suggesting the formation of "chiasmas" at the nodes of the contracting and condensing double spiral are noted. As a result of this combined untwisting, contraction and condensation of the double chromosomes, pachytene loops are formed, which, still in connection with the nucleolus at the base, form a "thick bouquet" remarkably similar to the like condition in animal cells. The arms of the loops now approach and become united to form the haploid number of pachytene bodies ("pseudo-reduction"). These decondense and the nucleus passes directly into a well-marked diffuse stage without a diplonema stage intervening.

At the end of the diffuse stage, the chromosomes once again make their appearance as twisted double strands, and pass into the "second contraction" stage. At the end of this stage they emerge in the *diploid* number, members of each pair connected *end-to-end*, thus exhibiting the phenomenon of diakinetic deconjugation. The univalents re-join each other in an end-to-end position ("telosyndesis") assume a side-by-side position secondarily and re-unite to form gemini. No tetrads seem to be formed.

The achromatic figure is intra-nuclear in origin and bipolar at all stages.

The metaphase, anaphase and telophase of the heterotypic division as well as the homeotypic division present no special features.

The nature of the synaptic union is discussed in some detail. The manner in which such union is brought about (para-or-telo-synapsis), and the significance in this connection of the pseudo-reduction observed in the formation of the pachytene bodies are pointed out, and in particular, the bearing of the phenomena of diakinetic deconjugation and re-union on the support claimed to be afforded in favour of telosynapsis by the behaviour of the chromosomes in the course of their emergence from the "second contraction" in *Oenothera* is discussed.

The origin and nature of the achromatic figure in the higher plants is next dealt with and the probable part played in its formation by the nucleolus is pointed out. The essential similarity between the so-called nucleolo-centrosome of the lower organisms and the nucleolus of the higher plants is indicated; some cases of *de novo* formation of centrosomes are reviewed; and the view is put forward that the centrosomal substance and the nucleolar substance are the same in their nature, both representing "fibrillar kinoplasm", centrosomes being kinoplasmic differentiations of a more or less permanent character which have become located in the cytoplasm and the nucleolus representing the main store located within the nucleus. It is suggested that the central apparatus is not "differentiated" in the case of the higher plants (except in the course of spermatogenesis in forms with motile sperms) because the need for it no longer exists. The belief that the centrosomal and nucleolar substances are essentially the same in their nature seems to be supported by the behaviour of the nucleolus observed in the early prophasic stages of meiosis in *Cyanotis*.

Explanations to the Figures.

The drawings are based exclusively on preparations stained in iron-haematoxylin and have been made with great care, using an Abbe *camera lucida.* A Leitz $\frac{1}{12}$ inch homogeneous immersion "fluorite" (semi-apochromatic) objective N. A. 1. 32 was used, with Huygen's eyepieces in the case of lower magnifications and "periplanatic" (compensating) oculars in the case of higher magnifications. A three-lens condenser N. A. 1. 40 was employed, also immersed.

In order to facilitate a comparison between the sizes of the nuclear cavity at various stages of the prophase, all drawings of these

stages (Figs. 1–36) have been made at the same magnification of 1900 diameters. Drawings of later stages are at lower magnifications noted separately in the case of each figure.

Mostly uncut nuclei have been drawn; where sections were drawn, this fact has been noted, when necessary.

Fig. 1. Nucleus starting on meiosis; some strands of the reticulum have begun to condense and thicken.

Fig. 2. Later stage; formation of chromocentres.

Fig. 3. Formation of leptotene threads from chromocentres; disappearance of reticulum.

Fig. 4. Beaded "spireme"; the nucleolus has shifted its position to a side of the nuclear cavity and close to the nuclear membrane; some of the strands of the spireme converge towards the nucleolus.

Fig. 5. "Polarized" leptotene loops; "thin bouquet".

Fig. 6. Synapsis; twisting of the leptotene threads.

Fig. 7. Early zygonema; the double chromosomes are flaccid and form curves.

Fig. 8. Zygonema later stage; the chromosomes are becoming stiffer and more erect.

Fig. 9. Zygonema, advanced stage; the chromosomes are stiff and stand up on the base formed by the nucleolus.

Fig. 10. Late zygonema; the chromosomes are preparing to enter into synizesis and form a tangle; observe spiral structure in the ends of two strands injured by microtome knife.

Fig. 11. Synizesis.

Fig. 12. Median section through nucleus in very early "open spireme", showing chromosomes being released from the contraction and the changes in shape and size undergone by the nucleolus.

Fig. 13. Tangential section through nucleus showing later stages of open spireme; observe the spiral twist at the cut end of one strand of the "spireme".

Fig. 14. Changes in the shape of nucleoli observed in early open spireme; the manner of attachment of the chromosomes is also shown.

Fig. 15. Section through nucleus, showing "break-down" of spireme in open spireme stage; the double-spiral structure of the spireme thread is clear.

Fig. 16. Section through nucleus showing an advanced stage in the untwisting, contraction, and condensation of the spireme threads; observe the double spiral structure as well as what looks like a fusion of the chromosomes at the nodes of the double spiral in the upper portions of the untwisting spireme thread.

Fig. 17 a. A single spireme thread at a stage later than that in Fig. 16: fusion of the two filaments composing the double spiral is clear at the nodes marked *n* and *nn*.

Fig. 17 b. One double chromosome in late stage of condensation, preparatory to the formation of the pachytene loops. The lozenge-shaped slits may effect a separation of the chromosomes to the right and left, in a plane different from that of the union (*i. e.*, a plane parallel to that of the paper).

Fig. 18. Entire nucleus showing a late stage of condensation preparatory to the formation of pachytene loops, corresponding to stage shown in Fig. 17 b.

Fig. 19. Formation of pachytene loops.

Fig. 20. Approximation and union of the two arms of the pachytene loops.

Fig. 21. "Thick bouquet", formed by the chromosomes which have become united in pairs; observe the nucleolus at the base.

Fig. 22. Uncut nucleus, showing the reduced number of pachytene bodies (fourteen) in polar view.

Fig. 23. Commencement of decondensation preparatory to the diffuse stage.

Fig. 24. Later stage of decondensation; chromomeres have once again made their appearance; the chromosomes have become detached from the nucleolus.

Fig. 25. Advanced stage of decondensation.

Figs. 26 and 27. Diffuse stage.

Fig. 28. Post-diffuse stage; observe the increase in the size of the nuclear cavity; the chromosomes have re-appeared and form twisted double strands.

Fig. 29. Second contraction.

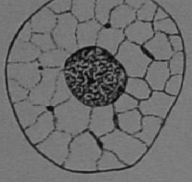
Fig. 30. Nucleoli in early second contraction.

Fig. 31. "Granular stage" succeeding second contraction.

Fig. 32. Bivalents arranged round the nucleolus; observe the slit between the two chromosomes in the case of some of the bivalents.

Fig. 33. Prediakinetic stage; deconjugation of the bivalents proceeding and univalents emerging into the nuclear cavity.

Fig. 34. Section showing nearly the whole of the nuclear cavity at a later stage than that shown in Fig. 33. Two bivalents have not yet deconjugated, ten chromosomes are emerging into the nuclear cavity as univalents, four pairs are engaged in re-assuming a side-by-side position and one pair shows the members which have already assumed a side-by-side position, thus accounting in all for 12 pairs of



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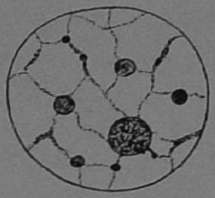

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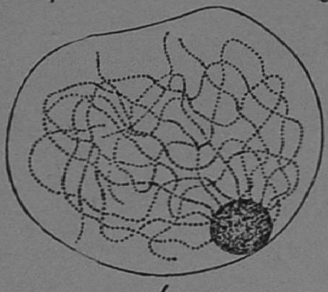

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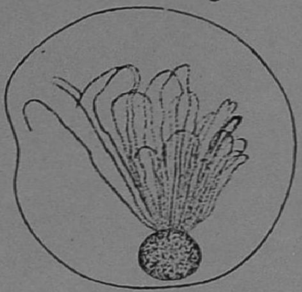

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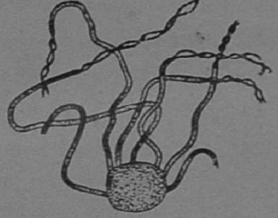

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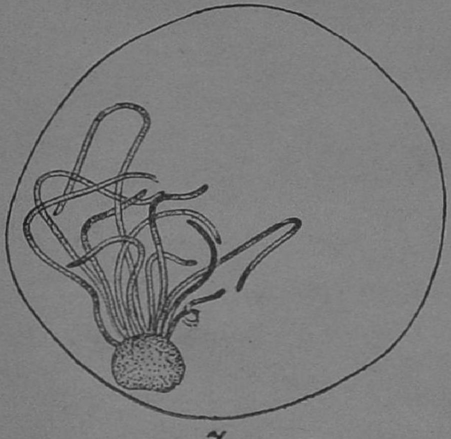

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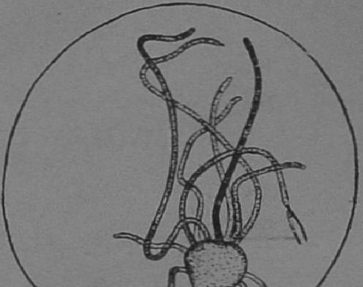

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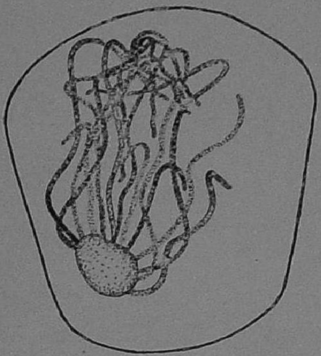

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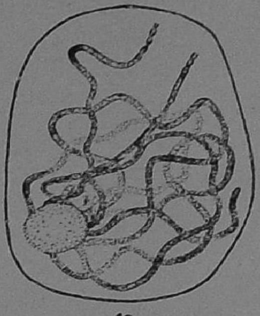

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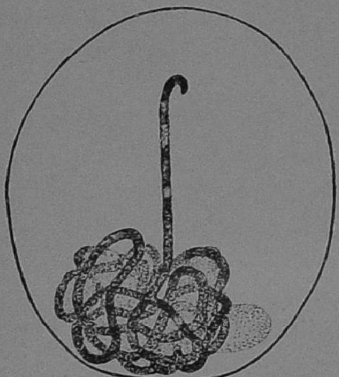

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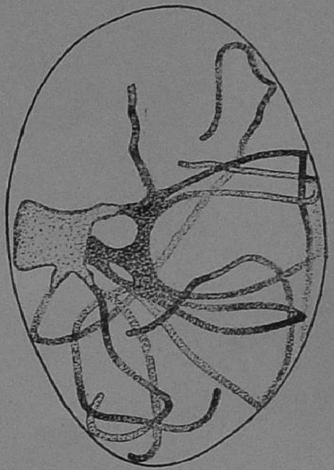

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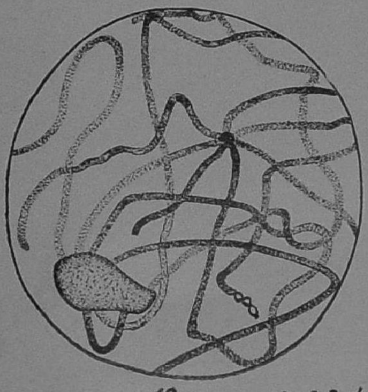

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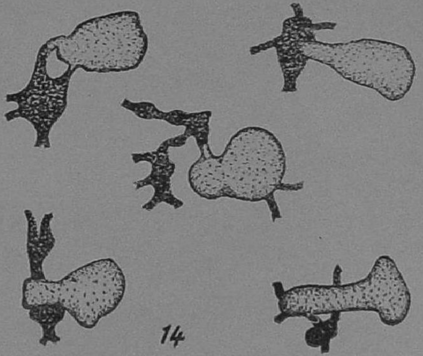

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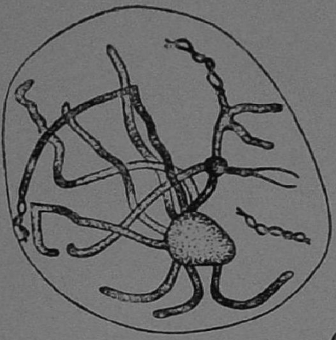

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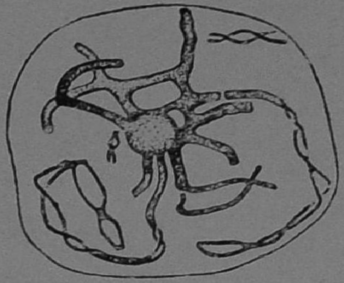

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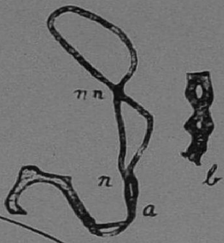

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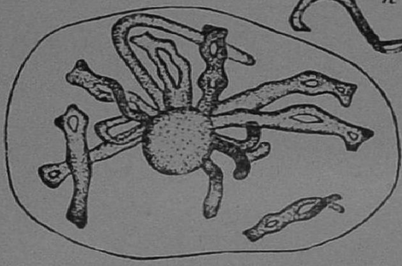

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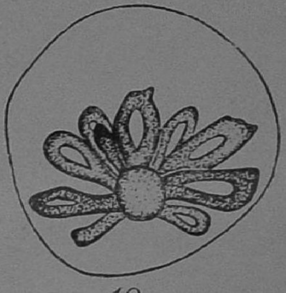

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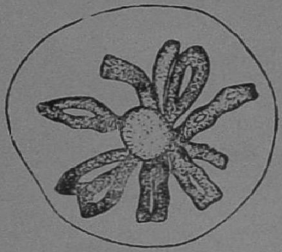

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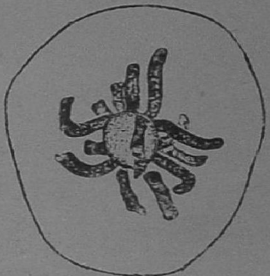

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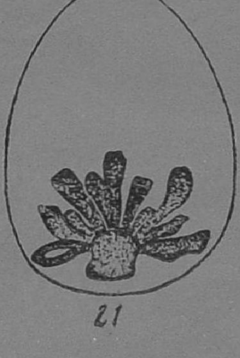

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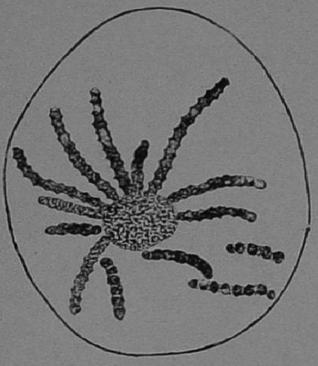

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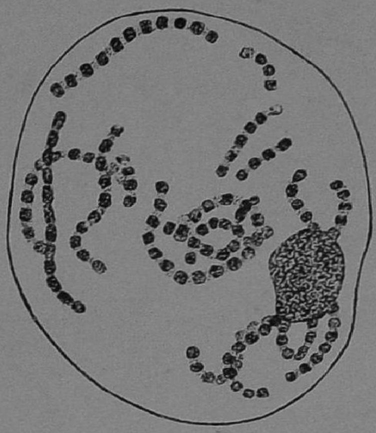

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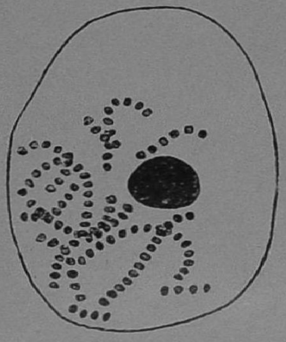

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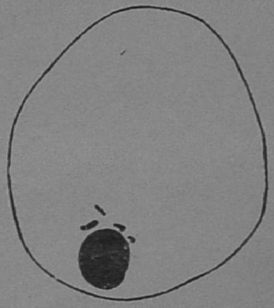

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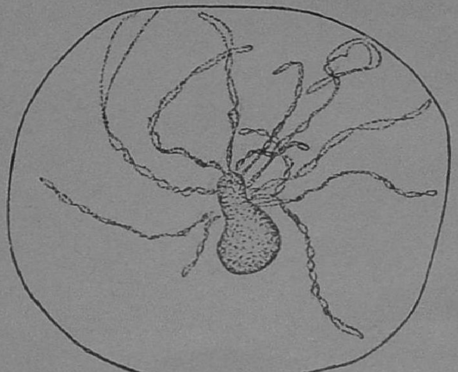

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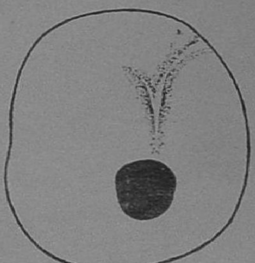

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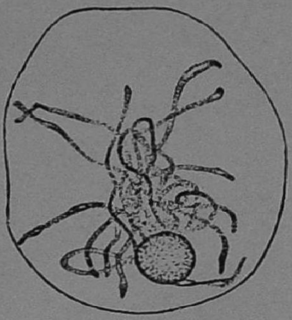

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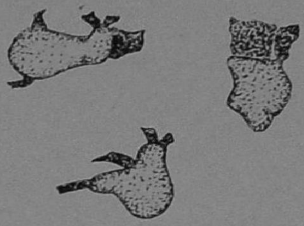

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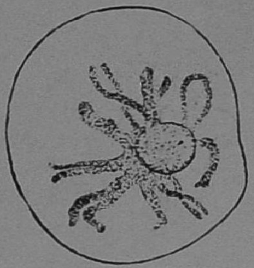

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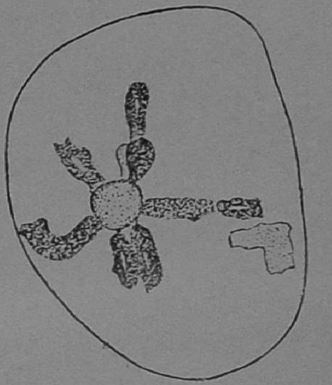

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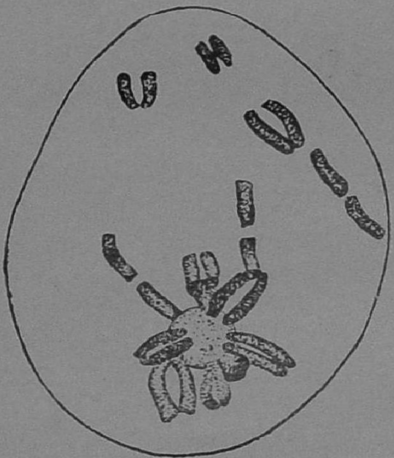

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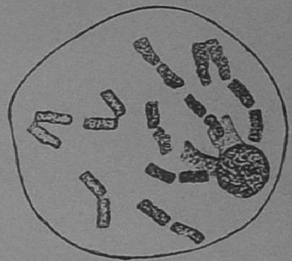

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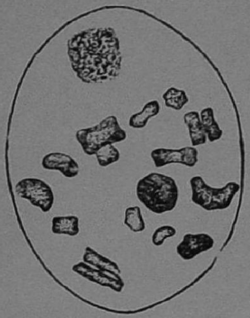

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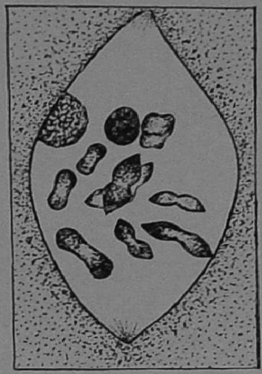

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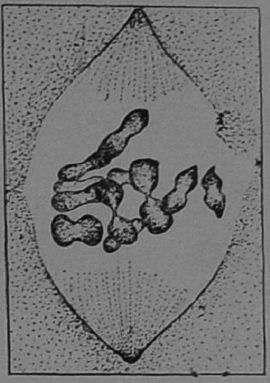

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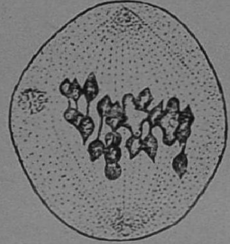

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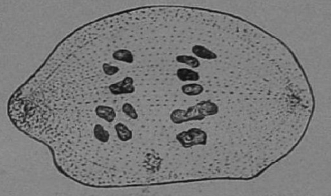

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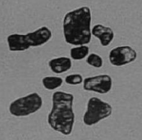

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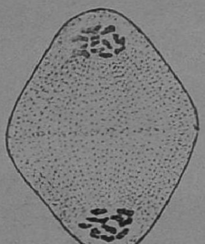

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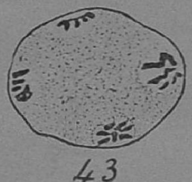

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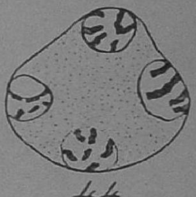

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chromosomes ; the other two pairs are missing from this section, having passed into the adjacent one. The full number of chromosomes are to be seen, however, in Fig. 33.

Observe that the univalents belonging to each pair, in emerging into the nuclear cavity take an end-to-end position with regard to each other.

Fig. 35. Diakinesis ; formation of gemini by union of univalents. Observe the chromidial body.

Fig. 36. Section through nucleus showing the origin of the achromatic figure ; the chromosomes have begun to collect at the equator of the nuclear cavity.

Fig. 37. Section through nucleus showing the origin of the achromatic figure, slightly later stage than that shown in Fig. 36. Chromosomes nearly all assembled at the equator of the nuclear cavity ; chromidial body being cast out of the nuclear cavity near the equator where the nuclear membrane first breaks down.

Fig. 38. Metaphase. × 1140.

Fig. 39. Metaphase group of chromosomes in polar view, earlier stage than that shown in Fig. 38. × 1140.

Fig. 40. Anaphase ; observe the elongation of the spore-mother-cell as a whole. × 1140.

Fig. 41. Telophase of heterotypic division. × 760.

Fig. 42. Group of chromosomes in telophase of heterotypic division, in polar view. × 1140.

Fig. 43. Section showing rather early stage of telophasic reconstruction in *homcotypic* division, observe that the cell-plate laid down in division I has disappeared. × 760.

Fig. 44. Same as in Fig. 43, but later stage. × 760.

VIRUS DISEASES OF THE TOMATO*

BY

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Prof. J. WESTERDIJK in 1910 first published her observations on the tomato mosaic. The nature of this mosaic proved to be rather different from that of the tobacco mosaic—the only type of such disease known at that time. One fact about this tomato mosaic especially threw the scientists into great puzzle. It was mentioned to be hereditarily transmissible through seed, whereas the tobacco mosaic was known as not seed-borne; and as all the then existing mosaic diseases were ascertained to be identical with the only existing tobacco mosaic, great attempts were done to prove the invalidity of the seed-transmission of the tomato mosaic. The problem thus becoming a complicated one, an effort is made here to disintricate it as much as possible.

We shall first, therefore, take a review of all the existing mosaic like diseases—the viruses of the tomato plant.

Apart from the tomato mosaic of WESTERDIJK, the ordinary tobacco mosaic is found to be infecting the tomato plant. Several workers are unanimous over this point and it is very easy to prove the existence of this virus through intracellular inclusions. The vacuolate bodies and the conspicuous albuminoid crystals stand as a criterion to this virus. This tobacco Virus No. 1 can be proved also by return grafts of tomato to tobacco. The characteristics of this virus are the same as the tobacco virus 1 and the modes of infection exactly similar in nature. This malady consequently is not transmissible through seed.

The tomato plant is extremely susceptible to several diseases existing on the solanacaeous plants. Many of such diseases are transmitted to this test by grafts. This case has been shown by several workers on the line. Evidence has come forward of late that a certain sort of tomato virus is damaging the green house crops in England. The writers have called this disease 'Tomato Yellows' or the Tomato-Aucuba Mosaic. DR. HENDERSON SMITH

* This article was written when the writer was working in the "Potato Research Labaratory" at Wageningen, Holland

believes it possibly identical with the yellow tobacco mosaic or the tobacco virus 6 of Johnson. It is distinguished from the ordinary tobacco mosaic by its strikingly conspicuous spectacular, yellow spots. No stem necrosis is seen. The only difference between this mosaic is in the activity of the supernatant fluid, which in the case remains active even after 70 per cent alcohol treatment. Otherwise, it is as infectious in character as the other virus diseases.

A very special virus is named as "tomato stem necrosis" by JOHNSON in his "Classification of Plant Viruses". As a matter of fact, the characters of this disease as described by him do not much differ from those of the "streak" on this plant. "Streak" or "stripe" as it is otherwise called is an extremely complicated malady and has been reported as early as 1885. On account of its complicated nature it has also been known as a "double virus" disease as when transferred to certain plants, it loses its "streak" character and produces only "mosaic" which has been specified as a symptom on tobacco and physalis by Johnson. The "streak" was once erroneously attributed to bacteria.

The complicated nature of streak in the tobacco and the tomato plant is also well known. There is no doubt, as to its independent existence in potato and tobacco; certain varieties of potato are found to be "masked" carriers of it. It can as well be transmitted by insects. And latest workers have brought forward proof of its appearance in a plant on introducing two sorts of viruses. Certain plants inoculated with "streak" have given only "mosaic" symptoms. We cannot discuss here all the pros and cons of the question, but we cannot but say that the stripe may be an independent virus or it may be an external sign of a mixture of several viruses. This remains as yet to be proved exactly. But all the results so far arrived at go to show that it is an infectious type of malady and the cause being unknown—of a virus type.

"A bunchy top" type of virus seems to be existing on the tomato crops of the Bombay Presidency in India. According to KULKARNI it appears in the fields and stunts the growth of the plant giving it perhaps a "witches'-broom" appearance. We cannot go into the details of this disease as the author is rather short in the descriptions of several "mosaic" diseases on different plants from India. But the "witches'-broom" of potato can be transmitted to the tomato plant by grafting. Whether this virus independently exists in the tomato plant is questionable.

It has been so far believed that a virus from a plant is transmissible only in that family. For instance, a tobacco virus may be infectious to members of solanaceous family and not to other plants. But this belief is strongly contradicted by the virus "Tomato Yellows". "Tomato Yellows" which is found in tomato crops growing side by side with sugar beet plantation is proved to be transmitted from the "Curly top of sugar beet" to the tomatoes by the leaf hopper Euteix tenella (Baker). So far known this disease is found to be existing in America.

Discussion.

From the above statement it will be clearly seen that there exist more than one virus disease on the tomato plant. A very great confusion is likely to occur as in some of these diseases external signs can hardly be trusted. It is a well-established fact now that there are several diseases of this type occurring on the potato and tobacco plant. And it will be quite necessary not to mingle these apparently like diseases of the tomato plant.

For the present we have to take Prof. Westerdijk's disease as a separate sort of one—from its distinguishing character of seed-transmissibility. Such seed-transmissible character does occur in several other sorts of diseases—especially those of fungi. But the *'porte'* of these mycological affectations of the plant is not a mysterious one as is found in those types of virus ones—nor is it questionable as these fungal organisms make themselves very conspicuous in any part of the plant. Such is not the case with virus type maladies. These severely infectious diseases can only be made out after their thorough invasion of the plant and that only by the external characters. Mosaic has been said to be seed transmissible in certain bean plants. But this seed-transmissibility of bean mosaic has been of late refuted (page 57, 1926 Rep. Dom. Bot. Canada).

It is also questionable that if such virus keeps itself alive in the dormant seed, then by multiplying vigorously in the growing seedling, why should it fail to kill the germinating seedling in its young growth. We are, therefore, at a very uncertain point on this question.

Some authors have doubted the careful handling of Miss Westerdijk's seedlings; indeed, twenty years ago it was not known that the virus is extremely resistant against ageing and this may be the reason what some sources of infections have been overlooked.

Another sign of the above virus is its 'Fern' or 'String' leaf character. It seems after the latest researches that this particular 'nervous' character of the leaf can be isolated from the 'mosaic' disease character. Nor this principle can be said to be strictly attached to a diseased condition of a plant as it is found in quite healthy plants. Several plants of healthy type do hide their lamina from the vision, leaving only veins and a strip of lamina. When this occurs in the potato plant, it is termed as the 'tomato leaf' of potato; and when it appears in the tomato, we call it "Fern leaf". Transmigration of soul, it is said, has much to do with the exchange of names.

A better example of confusion of such names is shown by the application of the term 'Aucuba' 'mosaic'. The term Aucuba mosaic has long been given to a potato malady by Prof. QUANJER. The characters of this disease as it occurs in potato are (1) its non-transmissibility by insects, (2) its not being severely infectious, (3) and it being non-filterable. These three characters do not hold good in the so-called "Aucuba" mosaic of tomato (a term applied by Beweley) which coincides in its characters with the infectious virus diseases. We can gather from the above statements that the Aucuba mosaic of potato resembles more the Abutilon Chlorosis, while the Tomato Aucuba resembles the "mosaic" viruses. The latter proves an economic terror to the farmer, while the former adds to the decorative sense of a horticulturist. One is non-filterable, the other is filterable. To avoid complicacy we suggest for the present the name NF—Aucuba mosaic for that of Tomato—the letters NF standing for its non-filterable character. The writer has in the summer of 1928 successfully transmitted the Aucuba mosaic of potato to the tomato (variety Waterbaby) through graft.

If this sort of intermingling of names is also the case in the Tomato mosaics is an open question as yet. In the beginning of 1928, the writer had an occasion to visit the Westland (in Holland) Greenhouse cultures of Tomatoes. A very conspicuous form of mosaic was seen to be existing there. Some plants were, therefore, brought to the laboratory at Wageningen and on cytological examination this virus was found to be the same as Tobacco mosaic number 1. Some grafts on tobacco were, therefore, made and the same cytological inclusions occurred, confirming therefore the identity of the Tobacco Virus 1. Not only this, but a casual plant of Solanum nigrum growing in the diseased Tomato plants gave the same internal and external signs.

It has been brought to the notice of the writer that occasional diseased plants occur in rows—leaving an interval of some healthy plants between. Workers associated with the virus diseases know that the disease does not get into the plant unless it is introduced into it by some means. We had a mosaic-diseased tobacco plant constantly growing in the green house. A few seed fallen from the pods of this plant, had germinated and the plants grew side by side, almost rubbing with the diseased plant in the same pot, and yet these plants remained healthy so long the writer had not rubbed the disease into them.

But the real problem begins when we know that there is no tobacco cultivation in the Westland Greenhouse parks. How is the disease introduced then? VALLEAU and JOHNSON have of late proved that tobacco mosaic is very easily transferred to tomato by the chewing and smoking habits of the workers. It seems probable that this must be the source of the disease in the Westland. Once the disease is introduced it can be easily taken up by other plants in transplantation.

Henderson Smith has shown recently that potato mosaic can also be successfully transmitted to tomato and that the 'Viroplasm' theory of JOHNSON does not hold good as he failed to obtain infection of healthy plants through the juice of healthy plants and consequently a doubt is expressed about the healthy state of Johnson's potatoes. It seems quite probable that JOHNSON's material might have been affected as our observation last summer on Green mountain potatoes received as healthy from America, showed that some of the potatoes proved to be mosaic affected. Recently, a relation between potato mosaic and Peach Yellows has been tried to be established by the same author. It might be very probable in America—such relation. But in Europe where potato virus has long been established, no such inter-relation has yet been known.

From the above review we can see that the virus problem in all these solanaceous transatlantic cousins of our plant-world although on its way to solution, is extremely complicated. We have tried, as far as possible, to give a definition of such diseases in tomato, but yet much remains to be disintricated.

Control.

For the virus-diseases of the mosaic type the same precautions ought to be taken. Fumigation to kill insects in the green houses is advisable. Once the disease is known sterilization of the soil

may be made and great cleanliness should be especially shown by the workers. A careful examination will explain the source of mosaic in the sort of tobacco used and principally this mark of tobacco should be avoided for workers to lay their hands on. Great care should as well be taken not to allow the same tools to be used with the healthy plants, with which a worker has already dealt with the diseased plants. A segregation of all diseased plants in a different green house is preferable as the product of these plants for consumption can be utilised. Besides for canning and other such products these affected tomato fruit does not do any harm. Weeding of unnecessary solanaceous plants growing in the surrounding is a precaution to be taken.

For "streak" Berkeley recommends "temperature at 70°F, steady watering, lessening or increasing the amount according to weather conditions, application of acid phosphates and controlling the richness of soil in nitrogenous fertilizers in the beginning so as to allow little need of it after the vigorous growth of the plants". To check the distribution of this disease by other means—certainly as in other virus diseases—will serve as an agenda from the writer.

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MICROSPOROGENESIS IN *CASSIA DIDYMOBOTRYA*

BY

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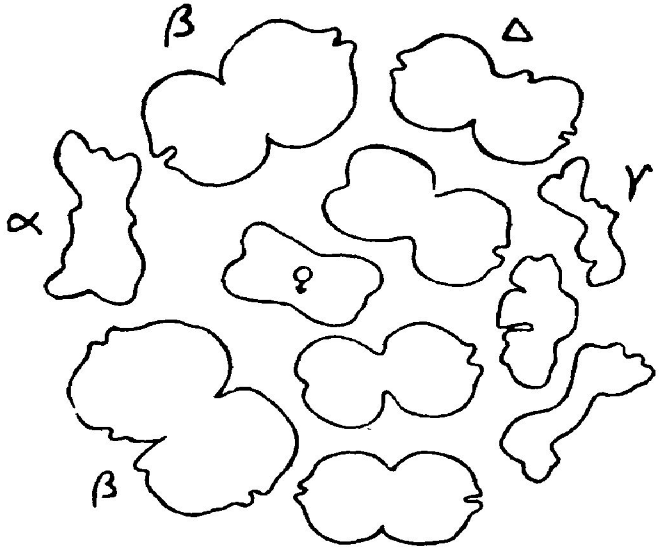
Introduction: Species of *Cassia* are being used in medicine since centuries. The genus *Cassia* has, therefore, been the recipient of a very fair amount of attention from systematists and pharmacologists. Bentham (1) gives the history of the genus. It seems strange that with the exception of Tischler's (12) paper on the nucleoplasmic ratio in the microspore mother cells, the present writer has not been able to hunt up any contribution on the cytology of this genus. It was partly to fill up this gap and partly to work out the fate of the nucleolus which is particularly large in the microspore mother cells that the present work was undertaken.

Montgomery (9) gave a review of the works on the nucleolus up to 1898. Wager (14) summarized the works up to 1904. Van Camp (13) has referred to papers published after 1904. Latter's (8) recent paper on *Lathyrus odoratus* has thrown abundant light on the behaviour of the nucleolus but much about this nuclear content is still shrouded in mystery.

Material and methods: The material for the present study was collected from plants growing in the Botanical Garden of the Government College, Lahore, in November and December, 1927. All the collections were made between 11-15 a. m. and 4-0 p. m. Bouin's fluid, Farmer's acetic-alcohol and the fluid used by Latter (8) were employed as fixatives. The flower buds after the removal of the calyx and corolla were usually kept in aceticalcohol for about 30 seconds before being put in the killing fluid. This was essential for expelling air from the buds which could not be removed by any other means. Hot fixatives were tried but with no improvement in fixation. Sections were cut between 5 and 11 microns. Heidenhain's iron-alum Haematoxylin with and without orange G as a contrast stain was used for staining.



TEXT-FIG. 1. × 60

Morphological: There are ten stamens in *Cassia didymobotrya* (text-fig. 1). Of these ten stamens one medium-sized stamen (a) is anterior. Two anteriolateral stamens (β), one on each side, are the largest in size. There are four medium-sized stamens (Δ), two on each side, which are posterio-lateral. Lastly, there are three small posterior imperfect stamens (γ).

Archesporium develops in the anthers of all the perfect stamens. Normal meiosis takes place and apparently fertile pollen grains are formed. In the anthers of the three imperfect stamens archesporium is not laid down at all. Invaginations along which dehiscence takes place are well developed in these imperfect stamens also. The microspore mother cells, their nuclei and the nucleoli of the latter are all uniform in size in all the perfect anthers. The difference lies in the number of the microspore mother cells contained within. They are far too many in the largest anthers than in the rest.

Early Archesporium: Early archesporial cells (Pl. I. Fig. 1) show a large nucleus which is 6 or 7 microns in diameter. The linin and the chromatin are rather scarce in the nucleus. There may be one, two or more nucleoli in the nucleus. The size and shape of the nucleoli varies. When there is a single large nucleolus its average diameter is about 3 microns. It stains deeply with haematoxylin and it has been seen connected by two or more thick dark processes with the nuclear membrane. In many cases, these

connections are swollen where they come into contact with the nuclear membrane. The nucleoli in the root-cells of *Phaseolus* have been described by Wager (14) to be similarly anchored by means of delicate threads.

The archesporial cells grow in size. The nucleolus within the nucleus of the archesporial cell also grows. In the early stages this growth is the result of fusion between smaller nucleoli to form a comparatively larger nucleolus. Later on the single nucleolus grows. This growth seems to take place at the expense of supplies passed from the cytoplasm into the nucleolus or by substances absorbed from the nuclear sap. But perhaps both of these processes may be taking place at the same time. The connections of the nucleolus with the nuclear membrane seem to support the first of the two above-mentioned alternatives.

From the structure of the nucleus and the staining capacity of the nucleolus it can be inferred that the major part of the chromatin is lodged within the nucleolus.

Tapetum: The tapetal cells are large, columnar and elongated at right angles to the wall of the anthersac. The cells are uni-nucleate to begin with. Their nuclei undergo typical mitotic divisions. Karyokinesis is not followed by cytokinesis and the cells become progressively binucleate, trinucleate and quadrinucleate. Latter (8) states that the tapetal cells in *Lathyrus odoratus* remain uninucleate throughout meiosis. The tapetal nuclei contain two or more nucleoli which are anchored to the nuclear membrane by means of stout processes.

The resting microspore mother cell: The microspore mother cells are polygonal in outline. They are closely packed within the anthersacs. Their cell-walls are thin. They are completely filled with cytoplasm. The cytoplasm shows an alveolar structure. No deep staining granules were seen in the cytoplasm. Each cell contains a spherical nucleus. In very few cases was the outline of the nucleus other than spherical. In each nucleus there is a single perfectly spherical nucleolus. The diameter of the nucleus is on an average between 9.7 and 10.5 microns. The diameter of the nucleolus is between 4.5 and 5.2 microns. A very diligent search was made for finding a mother cell with more than one nucleolus and out of the millions of cells which were studied with this aim only a very few showed two nucleoli. So the single large nucleolus may be considered typical of the microspore mother cell. This single nucleolus is formed by the fusion of the 2 or more

smaller nucleoli present in the nucleus of the young archesporial cell. Wager (14) found in *Phaseolus* that young root-cells had two or more nucleoli and as the cells approached maturity the nucleoli fused together so that in all the older cells only one nucleolus was found. The linin in the nucleus of the microspore mother cell is abundant, but it does not form a clear network. Several small rounded droplets of chromatin are found on the linin. The nucleolus is connected by strands with the nuclear membrane. These strands of linin if impregnated with chromatin are very much swollen where they come into contact with the nuclear membrane. The nucleolus stains very deeply and it does not part with its stain readily. From the subsequent behaviour of this nucleolus the writer concludes that it corresponds to the karyospheres of Wilson (15).

Heterotypic division: Without undergoing any kind of change the nuclear reticulum contracts towards one side of the nuclear cavity. There is absolutely no indication of parallelism in the linin threads before the nucleus contracts. Granules of chromatin are enclosed in the linin in an haphazard manner. Neither their number nor their size is very large. Prior to the contraction the nucleolus is seen attached to the linin and it remains so during the contraction. The nucleolus is never enclosed in the contraction knot but the two remain connected and are, therefore, in very close association while the contraction lasts. A deeply stained process issues forth from the nucleolus (Pl. I. Fig. 3). This process merges into the contraction knot. In mother cells destained to wash out the stain from almost all the chromatic particles the nucleolus showed a small body towards one side (Pl. I. Fig. 4). This body retains the stain persistently and remains black. This body always faces the collected mass within the nucleus. And it is this body which maintains a permanent connection with the contraction knot. It can be called the nucleolar body. During the contraction the amount of chromatin in the contracted mass seems to increase. This appears to take place at the cost of deep staining material passed out from the nucleolus. From the granules of chromatin present in the knot short and thin threads of chromatin are gradually organized (Pl. I. Fig. 5). During the later phases of this contraction these short and thin threads of chromatin become joined end to end to form a long and apparently continuous spireme. The chromomeres are very small and are arranged in a continuous series upon this thread. When the contraction is over the spireme uncoils itself and

becomes distributed throughout the whole of the nuclear cavity (Pl. I. Fig. 6). The spireme is very long and the whole of it is not sketched in this figure. The spireme remains connected with a papilla-like structure of the nucleolus. If the cells are washed to remove the stain from the spireme the nucleolar body becomes quite apparent and it seems to project out of the nucleolus to some extent. The situation can also be explained by assuming that the part of the spireme which is in contact with the nucleolar body stains as deeply as the nucleolar body itself and so the latter seems to project out of the nucleolus. This seems to be more appropriate because if chromatic material is being passed out of the nucleolus that part of the spireme immediately next to the nucleolus would naturally stain more deeply. The endonucleus described by Cleland (4) in *Oenothera franciscana* has been quite often seen connected with a part of the spireme. Latter (8) has described a similar body in the nucleolus of the microspore mother cell of *Lathyrus odoratus* which remains connected with the spireme during the early stages of the heterotypic prophase.

In a large majority of cases the writer has seen four threads radiating from the nucleolar body (Pl. I. Fig. 6). The writer explains this appearance by assuming that two points on the spireme maintain contact with the nucleolar body. At the same time throughout the prophase the nucleolus maintains its connections with the nuclear membrane (Pl. I. Fig. 8). From the persistent association of the nucleolus and the spireme and their reactions to stains it may be deduced that the nucleolus passes on its staining material to the spireme. It is not too much to suppose that the spireme moves in the nuclear cavity and every part of it passes along the nuclear body to receive its share of the staining material. The other alternative that the spireme remains stationary and the staining material passes along it from the nucleolus is well worth consideration.

The spireme is very long and very slender but later on due to the transfer for the staining material it thickens appreciably. It is placed along the periphery of the nucleus and no loops are visible. After some time the spireme becomes shorter in length and is seen thrown into loops. The loops are fairly numerous and in spite of repeated attempts the writer has not been able to count them (Pl. I. Fig. 7).

The spireme breaks into its constituent loops (Pl. I. Fig. 9). These are scattered throughout the nuclear cavity. When the spireme breaks into loops the attachment with the nucleolus is lost. The

nucleolar body has not been seen in the nucleolus at this stage. The nucleolus stains uniformly pale except in the region of its vacuoles where it is still paler. The loops are the fore-runners of the bivalent chromosomes (Pl. I. Fig. 10). From these comparatively long and slender segments the thick and short bivalents arise gradually (Pl. II. Fig. 11). The bivalents assume various forms. At the diakinesis stage the nucleolus stains very pale but its connections with the nuclear membrane are still present. The nucleolus is spherical and there is no diminution in its size. Its average diameter is 5 microns at this time. The present writer has never seen the nucleolus becoming amoeboid at this stage and it never becomes pressed against the nuclear membrane as in *Phaseolus* (14), *Oenothera* (4), *Clivia* (13) and *Lathyrus* (8). Besides the nucleolus and the bivalent chromosomes there is a certain quantity of a pale granular substance in the nucleus at this stage. This may be the residual substance which is not used in the formation of the chromosomes. From the appearance of the nucleolus it is quite apparent that all the deep staining material stored within it has been passed out to the chromosomes and that the nucleolus itself is quite empty.

Later, the nucleus is seen surrounded by a number of short fibres and the nuclear membrane disappears. It may be inferred that it gets resolved into these fibres. The nucleolus shows a diminution in size at this time. It measures about 3 microns in diameter. The fibres grow in length and are seen radiating from three or four centres (Pl. II. Fig. 12). The nucleolus has quite disappeared. Many workers have described that the nucleolus escapes into the surrounding cytoplasm when the nuclear membrane disappears. The present writer, as stated above, has seen it very much reduced in size during early spindle formation but he has never seen it escaping into the cytoplasm. His inference is that it is completely used up in the formation of the spindle fibres. Its connections with the nuclear membrane during late prophase lend further support to this inference. By these connections, perhaps, it is pulled out to form the spindle fibres. The fibres formed about the chromosomes gradually run in between them. By the convergence of the fibres of the multipolar spindle the bipolar spindle is formed.

Metaphase: When the achromatic figure is fully established the bivalent chromosomes are short rods and are distributed all over the equator of the spindle as seen in a polar view (Pl. II. Fig. 13). Several such polar views have been studied. The number of

bivalents is invariably 14. The attachment of the spindle fibres to the chromosomes is terminal in many cases (Pl II. Fig. 14). The double nature of the bivalents is not clear at the metaphase. The equatorial plate of chromosomes is surrounded by a hyaline zone. The cytoplasm shows two well marked zones about the spindle. The cytoplasm immediately surrounding the spindle is very granular and contains some small deep-stained particles. In the periheral zone of the cytoplasm many vaculoes are present and the number of deeply stained granules is very small.

Figure 15 (Pl. II) represents a very early anaphase. The univalent chromosomes are about to separate in this figure. Some of them show rather long tails at this time. Figure 16 (Pl. II) represents a later stage when the chromosomes have made some way towards the poles of the spindle. None of them show any tails at all. The tails have been withdrawn during the interval of time passed after their complete separation. In this figure towards one pole the full complement of 14 chromosomes is seen. Most of them appear to be spherical in form.

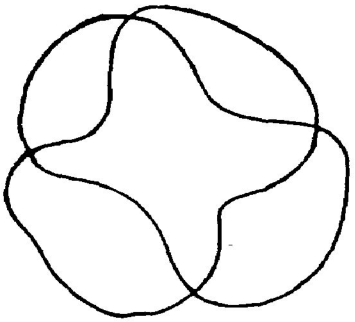
Telophase: On reaching the poles the chromosomes become longer than during the anaphase (Pl. II. Fig. 17), and it is not possible to follow the outlines of individual chromosomes. Later on the chromosomes show some attenuated extremities which anastomose and a very fragile nuclear membrane is seen about the daughter nucleus. The open network of the nucleus shows thick chromosomes and their deeply stained branches. (Pl. II. Fig. 18). There is absolutely no vacuolation of the chromosomes during telophase. The daughter nuclei grow in size to a large extent. The spindle fibres become inconspicuous and are absorbed by the cytoplasm. There is no indication of thickenings in the equatorial region of the spindle fibres. In the peripheral part of the cytoplasm many deep-stained granules are visible. As the nuclear membrane of the daughter nucleus becomes more firm, the reticulum formed by the chromosomes fails to take the stain deeply, but certain dark globules of chromatin are seen attached to it. Figure 19 (Pl. II.) represents the polar view of such a daughter nucleus. The small droplets of chromatin coalesce to form larger droplets. In course of time each nucleus shows only two very large spherical chromatin lumps, and besides there are some smaller chromatin granules on the reticulum (Pl. II. Fig. 20). If the stain is properly differentiated the appearance of these large chromatic bodies is exactly similar to the structure of the nucleoli in the microspore mother cells during prophase. The writer thinks that they are

nucleoli of the same type as those found in the mother cells. The two nucleoli found in each daughter nucleus may fuse to form one spherical nucleolus or they might remain separate. This single large nucleolus in each cell stains very deeply. The chromatin from the neighbouring chromatin granules seems to flow into it. Wager (14) has described the origin of nucleoli in the root cells of *Phaseolus* in an exactly similar way. Typical resting nuclei are thus developed after the heterotypic division. The daughter nuclei grow in size.

Homotypic division: The granules of chromatin found on the reticulum of the resting daughter nucleus grow in size presumably at the expense of the chromatin which flows out from the deep staining nucleolus during prophase (Pl. II. Fig. 21). The nucleolus is connected with the reticulum by strands along which the transfer of the chromatin takes place. Besides, the nucleolus is connected with the nuclear membrane by two very large processes (Pl. II. Fig. 21). The fully-formed prophasic chromosomes are short rods and they show longitudinal fission (Pl. II. Fig. 22). The nucleolus stains very faint pale, because it has passed out its chromatin, while the chromosomes stain very deeply. No spireme is organized during this prophase. The nucleolus remains spherical to the end of this prophase as during the prophase of the preceding heterotypic division. The spindle in this division is also multipolar in origin. No trace of the nucleolus is to be found at the metaphase. It seems probable that both the nuclear membrane and the faintly staining nucleolus are used up in the formation of the spindle fibres. The metaphasic chromosomes are shorter and thicker than prophasic chromosomes (Pl. II. Fig. 23). When moving towards the poles of the spindle during the anaphase the chromosomes are spherical in form (Pl. II. Fig. 24).

The chromosomes on reaching the spindle poles remain more or less spherical for some time (Pl. II. Fig. 25). Soon a nuclear membrane is seen about the grand-daughter nuclei (Pl. II. Fig. 26). Within each nucleus is seen a deep staining small nucleolus and particles of chromatin adhering to the linin net-work. This nucleolus is connected with the nuclear membrane by one or more processes (Pl. II. Fig. 26). It grows in size. The chromatin granules on the reticulum become fewer in number and their substance accumulates in the nucleolus (Pl. II. Fig. 27). The nucleolus stains very deeply. No thickenings are laid down on the spindle fibres in this division also and no cell-plate is formed.

When the telophasic changes of the homotypic division have progressed pretty far, furrows appear which cleave the mother cell into four spores. The first furrow develops between the daughter cells of the heterotypic division. This is very soon followed by the second furrow which separates the grand-daughter cells (Text-fig. 2). Farr (5) and several other writers have des-



TEXT-FIG. 2. × 1440.

cribed cytokinesis by furrows in many angiosperms. More recently, Castetter (3) has described cytokinesis by furrows in *Melilotus*. Castetter found that furrows are preceded by vacuoles in the equatorial region of the cells. There are no vacuoles in *Cassia* prior to the formation of the furrows.

When the four cells have been separated their nuclei become spherical. The nucleus of each cell contains a spherical nucleolus, very diffuse linin and a few chromatin particles. The nucleolus shows a dark internal body projecting a little towards one side (Pl. II. Fig. 28).

Chromosome numbers: The number of bivalent chromosomes, as stated above, is invariably 14. So the haploid and diploid numbers are 14 and 28 respectively.

Discussion: When the structure and the size of the early archesporial cell is compared with the structure and the size of the microspore mother cell, it becomes obvious that there is a very large increase in the size of the cell, its nucleus and the nucleolus of the latter. The increase in the size of the nucleolus is partly explained by the fusion of the smaller nucleoli in the nucleus of the young archesporial cell. This fusion is facilitated by the long period of rest which the mother cells undergo before entering upon the heterotypic division. Wager (14) has recorded that the nucleoli in the nuclei of the young root cells of *Phaseolus* fused

as the cells neared maturity. But this fusion by itself does not seem to explain adequately the phenomenal increase in the size of the nucleolus. The connections which the nucleolus maintains with the nuclear membrane till a very late stage in the prophase seem to warrant the passage of certain substances from the cytoplasm into the nucleolus. The final result of these changes is the formation of a single large spherical nucleolus in each mother cell.

Latter (8) mentions all those workers who have described that the nucleolus contributes material towards the formation of the chromosomes. Van Camp (13) came to the same conclusion after his elaborate study of *Clivia.* In *Cassia* the constant association of the spireme with the nucleolar body during the prophase of the heterotypic division and the later empty appearance of the nucleolus is strong proof of the passage of the stainable material from the nucleolus into the spireme. From the association of the spireme with the nucleolar body at two points as recorded in this study, it may be concluded that the spireme moves in the nucleus and its various parts pass along the nucleolar body and receive their share of the nucleolar contribution. Latter (8) also favours the same idea about *Lathyrus.*

The nucleolar body: This body has been recorded by Cleland (4) in *Oenothera* and he states that it is only occasionally connected with the spireme. "Usually, it lies freely in the nucleolus. It outlasts the nucleolus ordinarily". In *Lathyrus* (8) Latter has recorded the presence of crystal-like bodies in the nucleolus. No crystal-like bodies have been seen in *Cassia.* Latter (8) states that "the origin of the nucleolar body cannot be stated with certainty, but the evidence suggests that it is derived from the crystal body of the resting nucleus". In *Cassia didymobotrya* it becomes visible during early first contraction and disappears before the disappearance of the nucleolus. Latter (8) holds that the function of the nucleolar body "is to elaborate material and pass it on to the thickening spireme".

The nucleolus becomes pressed against the nuclear membrane during prophase in several plants, viz., *Phaseolus* (14), *Oenothera* (4), and *Lathyrus* (8). From this association of the nuclear membrane and the nucleolus Latter (8) deduces that some substances are passed into the nucleolus from the cytoplasm. As stated above, the nucleolus maintains its spherical form throughout and never becomes pressed against the nuclear membrane in *Cassia.* The presence of processes by which the nucleolus remains

connected with the nuclear membrane seem quite sufficient for the passage of material from the cytoplasm on to the nucleolus.

Gregory (7) after studying sweet-peas and Nichols (10) after studying *Sarracenias* came to the conclusion that the nucleolus serves as a storehouse for the bulk of the chromatin during the resting periods which intervene between successive mitoses. Flemmings (6) held that the nucleolus contributes material to the chromosomes. Definite proof for this has been adduced by Wager (14), Cardiff (2), Nichols (10), Cleland (4), Van Camp (13), Latter (8) and the present writer.

The most interesting point which the present writer has observed and which strengthens the above conclusion is the converse of it, i. e., the origin of the nucleolus from chromosomes and chromatic material during the telophase of the heterotypic division. This further supports the above conclusion.

A necessary corollary of these conclusions is that the linin 'serves as the morphological basis' of chromosomes while their staining substance resides in the nucleolus. This staining substance collects from the chromosomes into the nucleolus during the telophase and passes out during the succeeding prophase.

A noteworthy feature of Cassia didymobotrya is the absence of the second contraction from the prophase of the heterotypic division.

The homotypic division in *Cassia* is remarkable for the reason that it is preceded by typical resting nuclei. There is no formation of the spireme during the homotypic prophase.

Cytokinesis by furrows in *Cassia* adds another plant to the list of those dicotyledons in which furrows have been described by Farr (5) and others.

The majority of Leguminous plants examined show 6, 12, or 24 pairs of chromosomes (11). *Pisum* (11), and *Lathyrus* (8) are exceptions to this rule. *Cassia didymobotrya* is another exception with 14 and 28 chromosomes.

Summary.

The nucleoli in the archesporial cells are pretty large and are anchored to the nuclear membrane. They grow in size. The major part of the staining material is lodged within the nucleoli.

In the microspore mother cells there is a single very large deep staining nucleolus. It is connected with the nuclear membrane by strands.

During prophase the nucleolus shows a deep staining nucleolar body. This body remains connected with the contraction knot, while the first contraction lasts. The spireme which is organized in the nucleus remains connected with the nucleolar body. Staining material passes out of the nucleolus into the spireme. The spireme becomes looped. There is no second contraction. The spireme breaks into its constituent loops. The nucleolus becomes very pale and the nucleolar body cannot be seen. The nucleolus undergoes diminution in size and disappears. The number of bivalent chromosomes formed is invariably 14.

During telophase fresh nucleoli arise in the daughter nuclei. Chromatic material passes into these nucleoli. The nucleoli fuse and a single large nucleolus results in each daughter cell. This nucleolus is connected with the nuclear reticulum.

In the prophase of the second division staining material passes out of the nucleolus into the reticulum. After the staining material has been passed out, the nucleolus becomes faint and disappears. Fresh nucleoli arise in the grand-daughter cells. These are connected with the nuclear reticulum.

Cytokinesis takes place by furrows.

The chromosome numbers are 14 and 28.

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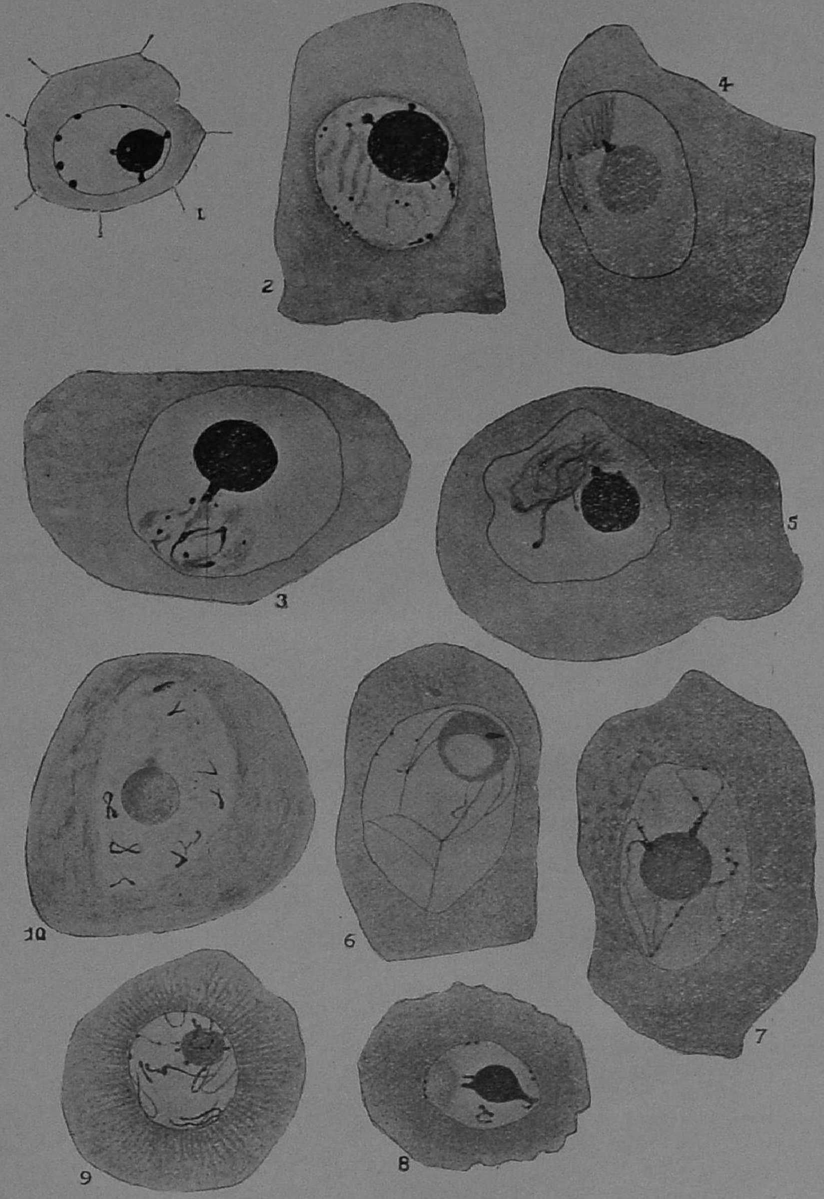
Explanation of Plates.

PLATE I.

Fig. 1. An early archesporial cell. × 2200.
Fig. 2. Resting microspore mother cell. × 2700.
Fig. 3. Microspore mother cell showing first contraction. × 2700.
Fig. 4. The same stage as in Fig. 3 but destained. × 2700.
Fig. 5. Later stage than that shown in Fig. 3 × 2700
Fig. 6. Mother cell showing open spireme. × 2200.
Fig. 7. Mother cell showing looped spireme. × 2700.
Fig. 8. Nucleolus showing connections with the nuclear membrane. × 1440.
Fig. 9. Spireme broken into looped segments. × 1440.
Fig. 10. Mother cell showing early bivalents. × 2200.

PLATE II.

Fig. 11. Bivalents. × 2200.
Fig. 12. Early spindle formation. × 2700.
Fig. 13. Polar view of metaphase. × 2700.
Fig. 14. Metaphase. × 2700.
Fig. 15. Very early anaphase. × 1440.
Fig. 16. Anaphase later than that shown in Fig. 15. × 1440.
Fig. 17. Early telophase. × 2700.
Fig. 18. Telophase. × 2200.
Fig. 19. Resting nucleus in one of the two daughter cells after the first division. Polar view. × 2700.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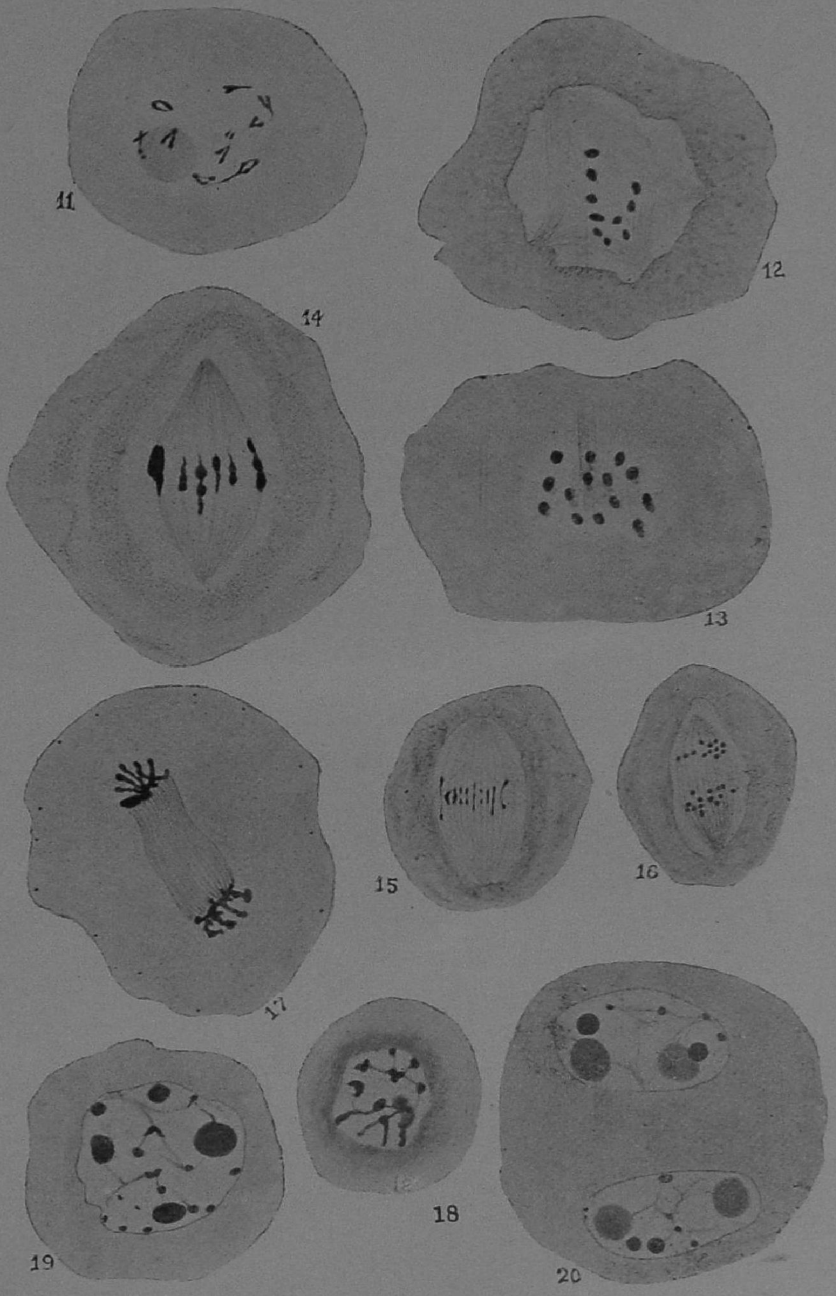
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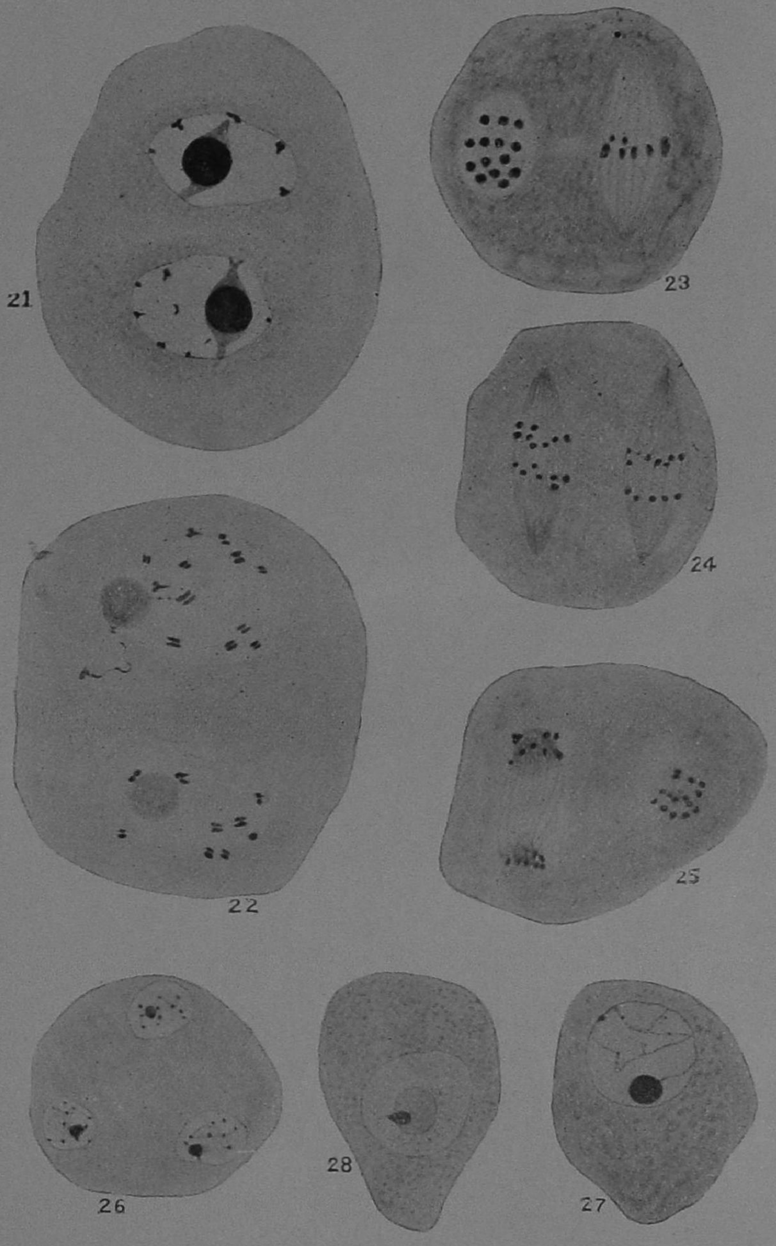
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Fig. 20. Resting nuclei in both the daughter cells after the first division. × 2700.

PLATE III.

Fig. 21. Second division. Early prophase. Nucleoli connected with the nuclear membrane. × 2200.

Fig. 22. Second division. Prophase showing split chromosomes. × 2700.

Fig. 23. Second division Metaphase. × 2200.

Fig. 24. Second division Anaphase. × 2200.

Fig. 25. Second division very early Telophase. × 2200.

Fig. 26. Resting nuclei in the microspore mother cell after the second division. × 1440.

Fig. 27. Microspore showing resting nucleus. × 2200.

Fig. 28. Microspore destained. × 2200.

A PROPOSED REVISION OF THE FLORA OF BRITISH INDIA

BY

E. BLATTER, S.J., PH.D., F.L.S.

Everybody doing systematic or floristic work in India must have felt the need of a revised edition of Hooker's Flora of British India or at least of a hand-list that indicates the many changes and additions that have been made since 1897 when the last volume of that great standard work of Indian Botany was published. It was a gigantic enterprise and it required a giant to supervise and complete it.

"The Flora of British India," says Hooker in the Preface to the 1st volume, "is intended to comprise within moderate compass brief descriptions, ordinal, generic and specific, of the Flowering plants and Ferns hitherto found within the British territories in India, together with those of Kashmir and Western Tibet; countries which, though outside that territory, belong to botanical regions included within it, which have been geographically and botanically explored by officers employed almost exclusively in the Indian service. . . . . . . It was originally intended to have included the Floras of Afghanistan and Baluchistan, as was done in the fragmentary 'Flora Indica', commenced in 1855 by Dr. T. Thomson and myself; but the plants of these countries having been recently included in Boissier's excellent 'Flora Orientalis' and belonging to quite another botanical region (the Occidental Asiatic), this intention has been abandoned."

The area, therefore, to be covered by the first volumes, was marked out very clearly. Not so for the later volumes. These contain a far more complete account of the flora. Hooker (Preface of Vol. VII) assigns two causes for this improvement: The extension of the area of British India in the interval and the many collections that were sent to Kew from entirely unknown or imperfectly explored regions of India during the same time. The greater part of Burma had fallen under British rule and large additions were made to the Indian Flora from that and other quarters, especially from the Malay Peninsula.

The treatment of the flora of India in the various volumes cannot, consequently, be considered to be uniform and a revision will have to include hundreds of species not mentioned in the first volumes.

Hooker, with the modesty of a true scientist, declares in the Preface to the last volume: The Flora of British India "aims at no more than being an attempt to sweep together and systematize within a reasonable time and compass, a century of hitherto undigested materials scattered through a library of botanical books and monographs, and preserved in vast collections, many of which latter had lain unexamined for half a century in the cellars of the India House, and in public and private herbaria. It is a pioneer work, which, besides enabling botanists to name with some accuracy a host of Indian plants, may, I hope, serve two higher purposes, to facilitate the compilation of local Indian floras and monographs of the large Indian genera; and to enable the phytographer to discuss the problems of the distribution of plants from the point of view of what is perhaps the richest, and is certainly the most varied botanical area on the surface of the globe, and one which, in a greater degree than any other, contains representatives of the floras of both the Eastern and Western Hemispheres."

That into a monumental work of this kind a number of errors should creep, is to be expected. Some local Indian Floras (Prain, Cooke, Gamble, Parker, Haines and others) and a good many monographs published in Europe and by the Botanic Gardens, Calcutta, have tried to correct such mistakes. But much remains to be done.

Nobody saw clearer the imperfections of the Flora of British India than Hooker himself. He was much concerned regarding the threatened suppression of the Saharanpur herbarium and botanist, and wrote on January 1901: "That N. W. India should be without the means of naming a plant by reference to a good Herbarium, would be a great blow to Indian Botany. As to the Fl. Brit. Ind. providing for this, it is absurd. That work is a hurried sweeping up of nearly a century of undigested materials, and is in no sense a Flora like Bentham's Australian. It had to be carried out in a reasonable time and except myself and Clarke none of my coadjutors was really well up in Indian botany, or authorities, or works, or climate, or geography. It is merely a crude guide to the extent and variety of the native vegetation of India. To have done Impatiens as it should have been, would have taken the time occupied by any one of the volumes." (L. Huxley, Life and Letters of Sir J. D. Hooker, II (1918) 387.)

When he was in need of a collection of Sikkim Impatiens he wrote to Gamble on 2nd March 1903: "I am now writing up detailed descriptions of the E. Nepal and Sikkim species, and still find errors of identification in my last review of them; and Fl. B. Ind. is past praying for in the matter of errors in detail, from bad

identifications, bad specimens and bad examination. I feel as if I were now only beginning to realize the difficulty of my undertaking such a genus at all." (Huxley l. c. 388).

I am not reproducing Hooker's own confessions in order to belittle his 'magnum opus'. Nobody has done more for Indian Botany than Hooker and nobody has done it better. All I wish to point out is that in spite of Hooker's Flora an immense amount of work in the domain of systematic and floristic work is facing us which after all forms the groundwork of the other departments of Botany.

Hooker's views on the question of nomenclature have necessitated a good many changes, and many more will have to be made, if we want to follow the international rules on this subject. "With regard to the vexed question," Hooker says "whether to attach to a species the name of the author who first described it, or of him who first put it into the genus to which I think that it belongs, I have adopted the latter alternative, chiefly on the principle that a right comprehension of genera is of higher importance than the power of describing a species. The number of species described by authors who cannot determine their affinities, increases annually, and I regard the naturalist who puts a described plant into its proper position in regard to its allies, as rendering a greater service to science than its describer, when he either puts it into a wrong place, or throws it into any of those chaotic heaps miscalled genera, with which systematic works still abound. I, however, admit that no laws or usages embrace all cases of disputed authority or priority, and that the best hitherto proposed are open to great abuses; but after many years' experience I find that the plan which, in common with the majority of botanists, I have followed, is open to the fewest objections, and does justice to the greatest and most deserving number of naturalists." (Fl. Brit. Ind. I, p. VII).

The international rules of botanical nomenclature adopted by the *International Botanical Congress of Vienna* came into force in 1905. European botanists follow those rules, but there still appear a number of publications in India in which their authors are sloth in drawing the necessary conclusions. Sometimes it is a kind of sentiment that does not want to give up an old name with which they have been familiar all their lives, in other cases, especially where popularising of botany is intended, the writers are afraid of changing a name, thinking that a new name will cause confusion and frighten the reader. We must admit that, for the time being, all these changes are inconvenient, even for the specialist, but the inconvenience will become much greater in the course of a number of years, and the confusion, resulting from going our own way may, after some time,

reach such a pitch that Indian and European botanists will find it difficult to understand each other or can follow each other only after a considerable loss of time spent in looking up and comparing synonyms. I don't think I am exaggerating when I say that more than half the time of a systematist in India is spent on this fruitless and uninteresting kind of work. The Paris Code of Nomenclature (1867), whose dominating spirit was Alphonse de Candolle, was right in laying down this principle in Article 1: "Natural History can make no real progress without a regular system of nomenclature, acknowledged and used by a large majority of naturalists of all countries."

What is to be done under the circumstances? It is evident that the time has not yet arrived for a complete revision of the Flora of British India. That time, considering the small number of workers in the field, is far off and none of us will live to see it, not even the youngest. And even after many years we shall not be able to say that the revision is final. As long as we work seriously and conscientiously we shall make progress, and progress necessarily involves changes.

What we can do is this: We can bring the Flora upto date, i.e., we can gather all the material that has accumulated during the last 30 years and write short monographs on the families or genera embodying the results obtained by previous botanists. Those results may be descriptions of new genera or species, notes as to the distribution of species, revisions of genera, changes in the arrangement of genera, transfer of species from one genus to another, suppression of species, combination of new species, nomenclatorial changes, etc., etc.

Instead of trying to explain in words what I exactly mean I give here a short revision of the family *Malpighiaceæ*. I have chosen this family, because it is a small one as far as it is represented in India, and because it has been monographed only two years ago, thus giving practically all the information we can desire.

I put the following pages before the readers of the Journal of the Botanical Society as a sample to be discussed and criticised by my colleagues and I shall request the Editor to publish the criticisms in the Journal. As I wish to start a work for the benefit of Indian and foreign botanists, I am very anxious to follow the best possible method. For this I require the help of my colleagues and I shall be grateful to them for any corrections, hints or suggestions.

I may mention that the area dealt with includes India, Burma and the Malay Peninsula. Should Baluchistan be added?

Malpighiaceae A. L. de Juss. Gen. Pl. (1789) 252; F. B. I. I, 417.

Genera 56, species ca. 800.—Tropics of Old and New World.

A. Principal wing of samara lateral
- I. Styles 3. No calycine glands ... 1. *Aspidopterys*
- II. Styles 1, rarely 2
  - 1. Calycine glands minute or absent ... 2. *Tristellateia*
  - 2. Calycine gland 1, large, adnate to pedicel ... ... 3 *Hiptage*

B. Principal wing of samara dorsal ... 4. *Brachylophon*

1. **Aspidopterys**, Juss. Malp. Syn. in Ann. Sc. Nat. 2. ser. Bot. XIII (1840) 266; F. B. I. I, 419.

Species 17, Indian 11.

A. Panicles composed of corymbs. Flowering peduncles and pedicels more or less elongate, slender, filiform. Bracts and bracteoles linear-lanceolate. Lateral wing of samara orbicular or broadly ovate
- I. Petals oblong or oblong-ovate, 6–7 mm. long. Ovary glabrous
  - (a) Peduncles bibracteolate at or below the tip
    - α Leaves cordate ... ... 1. *A. tomentosa*
    - β Leaves ovate, acuminate ... 2. *A. concava*
  - (b) Peduncles bibracteolate below the middle or above the base ... 3. *A. canarensis*
- II. Petals obovate, 4–5 mm. long. Ovary hirsute except in *A. oxyphylla* ...
  - (a) Mature leaves glabrous on both sides. oblong-ovate. Ovary glabrous ... ... 4. *A. oxyphylla*
  - (b) Also mature leaves subsericeous-woolly beneath, cordate. Ovary hirsute
    - α Leaves gradually up to 1–3 cm. acuminate
      - * Leaves more or less chartaceous, slightly revolute. Ovary sericeous ... ... 5. *A. lanuginosa*
      - Leaves membranous, not revolute. Ovary hispid ... 6. *A. nutans*
    - β Leaves suddenly up to 6 cm. acuminate ... ... 7. *A. cordata*

B. Panicles composed of more or less umbelliform corymbs or true umbels. Flowering peduncles and pedicels mostly short and stoutish. Lateral wing of samara lanceolate or oblong.

I. Flowering peduncles bibracteolate at or below the middle. Flower-buds oblong. Ovary densely hirsute. Wing of samara linear-oblong ... 8. *A. indica*

II. Flowering peduncles bibracteolate at the base. Flower-buds oval. Wing of samara lanceolate or oblong

(*a*) Hairs sericeous, magnetacicular. Leaves membranous

α Leaves rotund at the base, ovate, obovate or oval ... 9. *A. glabriuscula*

β The larger leaves more or less cordate at the base, orbicular ... 10. *A. orbiculata*

(*b*) Hairs hispid, biforked, one arm up to 3 mm. long, the other scarcely 0.2 mm. ... ... 11. *A. hirsuta*

1. **A. tomentosa** (Blume) Juss. in Ann. Sc. Nat. 2. ser. Bot. XIII (1840) 267; F. B. I. I, 422; Kurz For. Fl. I (1877) 175; Niedenzu in Engl. Pflanzenr. IV, 141, pt. I (1928) 21, fig. 8, B-D.—*Hiraea tomentosa* Blume in Bijdr. Fl. Nederl. Indie (1825) 225.— *A. costulata* Pierre Fl. For. Coch. XVII, fasc. (1892) pl. 275.—*A. obcordata* Hemsl. in Hook. Ic. Pl. IV, ser. VII (1900) t. 2673.—*Ryssopterys rufescens* Turcz. in Bull. Soc. Nat. Mosc. (1863) 583.—? *Aspidopterys Hutchinsonii* Haines in Kew Bull. (1920) 66.

Distribution: Orissa, Burma.—S. China, Cochinchina, Siam, Java.

2. **A. concava** (Wall.) Juss. l. c. 263; F. B. I. I, 420; Kurz For. Fl. I (1877) 175; Niedenzu l. c. 22.—*Hiraea concava* Wall. Pl. As. Rar. I (1830) 13.—*H. merguensis* Wight Ill. I (1838) 139.—*Aspidopterys Helferiana* Kurz For. Fl. I (1877) 176.—*Ryssopterys ovata* Turcz. in Bull. Soc. Nat. Mosc. (1863) 583.—*Aspidopterys ovata* Merrill et Rolfe in Philipp. Journ. Sc. III (1908) (*synonymum a cl.* Merrill. Enum. Philipp. Fl. Pl. II (1923) 380 *ad A. ellipticam translatum*).—*A. elliptica* Merrill l. c.—*Combretum sexalatum* Merrill in Philipp. Journ. Sc. I (1906) Suppl. 212, *quoad fruct.*, ex Merrill l. c.

Var. **Helferiana** (Kurz) Niedenzu in Arb. Bot. Inst. Ak. Braunsb. VI (1915) 7 *et* Engl. Pflanzenr. IV, 141 part I (1928) 24.—*A. Helferiana*

Kurz in Journ. As. Soc.) Beng. 3. II (1874) 137 *et* For. Fl. I (1877) 176.—*A. andamanica* Hutch. in Kew Bull. (1917) 99; Parkins. Fl. Andaman Isles. (1923) 107.—*A. elliptica* Merrill Enum l. c. (*partim*).

Distribution: Andamans, Tenasserim, Burma.—Philippines.

3. **A. canarensis** Dalzell in Hook's Journ. Bot. III (1851) 37; F. B. I. I, 420; Cooke Fl. Bomb. I (1901) 159; Talb. For. Fl. Bomb. I (1909) 181, fig. 111; Gamble Fl. Madras I (1915) 129; Niedenzu in Engl. Pflanzenr. IV, 141 pt. I (1928) 26—*A. glomerata* Wight Ic. VI (1853) t. 1986.

Distribution: Konkan, N. and S. Kanara, Mysore, W. Ghats, Malabar to Tinnevelly.

4. **A. oxyphylla** (Wall.) Juss. in Ann. Sc. Nat. 2. ser. Bot XIII (1840) 267; Niedenzu in Engl. Pflanzenr. IV, 141, pt. I (1928) 26.—*Hiraea oxyphylla* Wall. Cat. (1828) 7264.—*Aspidopterys Roxburghiana* Hook. f. in F. B. I. I, 420 (*partim*); Cooke Fl. Bomb. I (1901) 158; Talb. For. Fl. Bomb I (1909) 118.—*A. glabriuscula* Niedenzu in Arb. Bot. Inst. Ak. Braunsb. VI (1915) 9.

Distribution: Sylhet, Khasia Hills.

5. **A. lanuginosa** (Wall.) Juss. in Ann. Sc. Nat. 2. ser. Bot. XIII (1840) 267; Niedenzu in Engl. Pflanzenr. IV, 141, pt. I (1928) 26.—*Hiraea lanuginosa* Wall. Pl. As. Rar I (1830) 13 *et* in Cat. (1830) no. 1058 (*partim quoad spec. foliis villosis*).—*Aspidopterys nutans* Hook. f. in F. B. I. I, 421 (*partim*).—*A. Roxburghiana, forma* Hosseus in Beih. Bot. Zentralbl. XXVIII, 403.

Distribution: Nepal, Sikkim, Siwalik, East Bengal, Assam, Upper Burma.—Siam.

6. **A. nutans** (Roxb.) Juss. in Ann. Sc. Nat. 2. ser. Bot. XIII (1840) 267; F. B. I. I (1872) 421 (*partim*); Kurz For. Fl. I (1877) 175; Niedenzu in Engl. Pflanzenr. IV, 141, pt. I (1928) 27.—*Hiraea nutans* Roxb. Hort. Beng. (1814) 34 *et* Fl. Ind. II (1821) 448; Wall. Pl. As Rar. I (1830) 13.—*Aspidopterys Wallichii* Hook. f. in F. B. I I (1872) 421.

Distribution: Central and N. W. Himalaya.

Var. **typica** Niedenzu in Arb. Bot. Inst. Ak. Braunsb. VI. (1915) 11.

Distribution: Kumaon, N. W. Himalaya.

Var. **Wallichii** (Hook. f.) Niedenzu l. c.—*A. Wallichii* Hook. f. l. c.

Distribution: Kumaon, Siwalik and Jaunsar Divis., Dehra Dun, Saharanpur, Garhwal, Sikkim.

7. **A. cordata** (Heyne) Juss. in Ann. Sc. Nat. 2. ser. Bot. XIII (1840) 267; Hook. f. in F. B. I. I (1872) 421; Cooke Fl. Bomb. I

(1901) 158; Talb. For. Fl. Bomb. I (1909) 181; Niedenzu in Engl. Pflanzenr. IV, 141, pt. I (1928) 28.—*Hiraea cordata* Heyne in Wall. Cat. (1828) 1060; Wall. Pl. As. Rar. I (1830) 13.

Distribution: Bombay Pres., Konkan, Deccan, N. Kanara, S. M. Country, Bellary, Mysore.

8. A. **indica** (Roxb.) Hochreut. in Bull. Inst. Bot. Buitenz. XIX (1904) 45; Niedenzu in Engl. Pflanzenr. IV, 141, pt. 1 (1928) 29.—*Triopteris indica* Roxb. Cor. Pl. II (1798) 32, t. 160; Willd. Sp. Pl. II (1799) 744, n. 2.—*Hiraea indica* Roxb. Hort. Beng. (1814) 90. *et* Fl. Ind. II (1832) 448.—*Aspidopterys Roxburghiana* A. Juss. in Ann. Sc. Nat. ser. 2. Bot. XIII (1840) 267; F. B. I. I, 420, *excl. vars. et syn.*; Kurz For. Fl. I (1877) 176.

Distribution: W. Peninsula of the Madras Pres.

9. A. **glabriuscula** (Wall.) Juss. in Ann. Sc. Nat. 2. ser. Bot. XIII (1840) 267; Niedenzu in Engl. Pflanzenr. IV, 141, pt. I (1928) 29.—*Hiraea glabriuscula* Wall. Cat. (1828) 260, n. 6626.—*Aspidopterys Roxburghiana* var. 2 *glabriuscula* Hook. f. in F. B. I. (1872) 420.—*A. oxyphylla* Niedenzu in Arb. Bot. Inst. Ak. Braunsb. VI (1915) 13.

Var. **subrotunda** Niedenzu l. c.—*Aspidopterys Henryi* Hutch. in Kew Bull. (1917) 94.

Distribution: Assam.—Yunnan, Philippines.

Var. **brevicuspis** Niedenzu l. c.—*Aspidopterys floribunda* Hutch. in Kew Bull. (1917) 95.

Distribution: Sikkim, Bhutan, Khasia, E. Bengal, Manipur.—Yunnan.

Var. **longicuspis** Niedenzu l.c.

Distribution: Assam, E. Bengal.

10. A. **orbiculata** (Roxb.) Niedenzu in Arb. Bot. Inst. Ak. Braunsb. VI (1915) 14 *et* in Engl. Pflanzenr. IV, 141, pt. 1 (1928) 31.—*Hiraea orbiculata* Roxb. Hort. Beng. (1914) 90; Wall. Pl. As. Rar. II (1831) 13.—*H. rotundifolia* Roxb. Fl. Ind. II (1832) 448.—*Aspidopterys rotundifolia* Juss. in Ann. Sc. Nat. 2. ser. Bot. XIII (1840) 267.

Distribution: Sikkim, Khasia.

11. A. **hirsuta** (Wall.) Juss. in Ann. Sc. Nat. 2. ser. Bot. XIII (1840) 267; Hook. f. in F. B. I. I (1872) 421; Kurz For. Fl. I (1877) 176; Niedenzu in Arb. Bot. Inst. Ak. Braunsb. VI (1915) 15 *et* in Engl. Pflanzenr. IV, 141, pt. 1 (1928) 31.—*Hiraea hirsuta* Wall. Pl. As. Rar. I (1830) 13, t. 13, *et* Cat. 1059.

Distribution: Burma, Siam.

2. **Tristellateia** Thouars Gen. nov. Madagasc. (1806) 14, n. 47; F. B. I. I (1872) 418.

Species 17, Indian 1.

1. **T. Australasiae** A. Rich. Sert. Astrolab. (1833) t. 15, *postea australasica* auct. F. B. I. I (1872) 418; Niedenzu in Engl. Pflanzenr. IV, 141, pt. I (1928) 60; Ridley Fl. Mal. Penins. I (1922) 327, fig. 32.—*T. australia* A. Rich. Sert. Astrolab. (text.) II (1834) 38.—*Platynema laurifolium* Wight & Arnott in Edinb. New Philos. Journ. (1833) 179 *et* Prodr. (1834) 107.—*Hiraea reclinata* Blanco *Fl.* Filip. (1837) 378 (*non* Jacq.) *ex* Merrill. Spec. Blancoan. (1918) 107.—*Tristellateia malintani* Blanco Fl. Filip. ed. 2 (1845) 267, ed. 3. II (1878) 132, t. 135.

Distribution: Singapore, Malacca.—Siam, Cochinchina, Malay Archipelago, New Guinea, Philippines, Formosa.

3. **Hiptage** Gaertn. Fr. et sem. pl. (1791) 169, t. 116; F. B. I. I. 418.

Species about 25, Indian 7.

A. Limb of petals lacero-fimbriate	
I. Lateral wings of samara linear, the apical one almost twice as long, oblanceolate-linear	1. *H. malaiensis*
II. Lateral wings obovate, the apical one 2–5 times longer, oblanceolate	
1. Racemes 10–30-flowered, axillary, including the peduncle 0.5-2 cm. long	
(*a*) Leaves lanceolate or ovate, more or less long-acuminate. Dorsal comb of samara short ...	2 *H. benghalensis*
(*b*) Leaves obovate or oval or ovate, abruptly, shortly and obtusely acuminate. Dorsal comb of samara up to 11 mm. long and 3 mm. broad	3. *H. obtusifolia*
2. Racemes short, 4–16 flowered, up to 7 forming a leaf-bearing panicle ...	4. *H. parvifolia*
B. Limb of petals only denticulate	
I. Leaves lanceolate, long-acuminate, glabrous on both sides	
1. Racemes fascicled. Calycine gland ovate-oblong ...	5. *H. acuminata*
2. Racemes ending the many-leaved branchlets. Calycine gland linear...	6. *H. sericea*
II. Leaves ovate, acute or obtuse or abruptly and shortly acuminate at the apex ...	7. *H. candicans*

1. **H. malaiensis** Niedenzu in Arb. Bot. Inst. Ak. Braunsb. VI (1915) 39 *et* in Engl. Pflanzenr. IV, 141, pt. I (1928) 76.

Distribution : Perak.

2. **H. benghalensis** (Linn.) Kurz in Journ. As. Soc. Beng. XIV, 2 (1879) 36 *et* For. Fl. I (1877) 173 ; Niedenzu in Arb. Bot. Inst. Ak. Braunsb. VI (1915) 40.—*Banisteria benghalensis* Linn. Sp. Pl. I (1753) 427, n. 4.—*B. tetraptera* Sonnerat Voy. Ind. Or. II (1782) t. 135.—*B. unicapsularis* Lam. Encycl. Méth. Bot. I (1783) 367, n. 5.—*Molina racemosa* Cav. Diss. IX (1790) 435, t. 263.—*Hiptage Madablota* Gærtn. Fruct. et Sem. Pl. II (1791) 169, t. 116 ; Wight & Arn. Prodr. (1834) 107 ; Wight Illustr. (1838) t. 50 ; Hook. f. in F. B. I. (1872) 418 ; Kurz For. Fl. I (1877) 173 ; Cooke Fl. Bomb. I, 157 ; Talb. For. Fl. Bomb. I (1909) 178, fig. 110 ; Gamble Fl. Madras (1915) 128 ; Ridley Fl. Malay Penins. I (1922) 328.—*Gaertnera racemosa* Roxb. Pl. Corom. I (1795) t. 18 *et* Fl. Ind. II (1832) 368.—*Succosvia fimbriata* Dennst. Schlüssel z. Hort. Malab. (1818) 32.—*Hiptage pinnata* Elmer Leafl. Philipp. Bot. V (1913) 1810.

Distribution : Throughout the hotter parts of India, from Jammu and Sind to Burma, Malacca and Ceylon.—Malay Archipelago eastwards to Formosa and the Philippines, China.

3. **H. obtusifolia** (Roxb.) DC. Prodr. I (1824) 583 ; Kurz. For. Fl. I (1877) 173 ; Niedenzu in Engl. Pflanzenr. IV, 141, pt. I (1928), 79.—*Gaertnera obtusifolia* Roxb. Catal. Calcutt. (1814) 32.

Distribution : Nilgiris, Saharanpur, Penang, Andamans.—China, Formosa, Java.

4. **H. parvifolia** Wight and Arn. Prodr. (1834) 107 ; Hook. f. in F.B.I., I, 419 ; Gamble Fl. Madras (1915) 128 ; Niedenzu in Engl. Pflanzenr. IV, 141, pt. I (1928) 79.—*Hiptage Cumingii* Merrill in Philipp. Journ. Sc. Bot. V (1910) 190.—*H. Loheri* Merrill Spec. Blancoan. (1918) 213.—*Triopteris jamaicensis* Blanco Fl. Filip. (1837) 350 (*non* Linn.).—*Hiptage madablota* F. Vill. Noviss. App. (1880) 32.

Var. **typica** Niedenzu l.c. 80.

Distribution : Mysore, Tinnevelly, S. Travancore, Khasia Hills, Ceylon, China, Timor.

5. **H. acuminata** Wall. Cat. (1828) 1065 ; Hook. f. in F.B.I. I (1872) 419 ; Niedenzu in Engl. Pflanzenr. IV, 141, pt. I (1928) 80.

Distribution : Bengal, Khasia Hills, Burma.

6. **H. sericea** (Wall.) Hook f. in F. B. I., I (1872) 419 ; Niedenzu in Engl. Pflanzenr. IV, 141, pt. I (1928) 81 ; Ridley Fl. Malay Penins. I (1922) 328.—*Clerodendron sericeum* Wall. Cat. (1828) 1814.—*Hiptage parviflora* Wight Cat. (1833) 358.

Distribution : Penang, Malacca,-China.

7. **H. candicans** Hook. f. in F.B.I., I (1872) 419; Kurz. For. Fl. I (1877) 174; Niedenzu in Engl. Pflanzenr. IV, 141, pt. I (1928) 82.—*H. arborea* Kurz in Journ. As. Soc. Beng. (1873) 228.

Var. **parvifolia** Pierre Fl. Forest. Cochinch. fasc. XVII (1892) 271; Niedenzu l.c. 82.

Distribution: Burma (Pegu, Mandalay).—Cochinchina.

4. **Brachylophon** Oliver in Hook. Ic. Pl. (1887) t. 1566 (not in F.B.I.).

Species about 4, Indian 1.

1. **B. Curtisii** Oliver in Hook. Ic Pl. (1887) t. 1566; Niedenzu in Engl. Pflanzenr. IV, 141, pt. II (1928) 250; Ridley Fl. Malay Penins. I (1922) 329.

Distribution: Penang.

Var. **Hullettii** Ridley Fl. Malay Penins. I (1922) 329.—*Brachylophon Hullettii* King in Journ. As. Soc. Beng. 62, II (1893) 196.

Distribution: Malacca.

Var. **Scortechinii** Blatter.—*Brachylophon Scortechinii* King in Journ. As. Soc. Beng. 62, II (1893) 197.

Distribution: Perak.

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BY

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AND

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